A STUDY OF THE DEVELOPMENT OF THE HEAD AND PHARYNX OF THE LARVAL URODELE *HYNOBIUS* AND ITS BEARING ON THE EVOLUTION OF THE VERTEBRATE HEAD

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[Plates 5 to 7]

CONTENTS

The early development of the head and pharynx of *Hynobius nebulosus* (11·5 to 32 mm long) and *retardatus* (27 and 37 mm specimens) was investigated in some detail from transverse serial microtome sections. Analysis included the chondrocranium, jaws and hyobranchial skeleton, ossifications, cranial and anterior spinal nerves, musculature, blood system and other associated anatomical features.

The structure of the skeletogenous elements in general agreed with earlier descriptions. However, a rudimentary fenestra lateralis nasi is found in the nasal capsule of *H. nebulosus*, hitherto not reported, and a complete cartilaginous processus pterygoideus, confluent with the trabecula and inner margin of the lamina orbito-nasalis described by Edgeworth (1923*a*), was not extant in any *Hynobius* specimen. *H. retardatus* has a hypoglossal foramen (and nerve) and joins *H. nebulosus* (Fox 1957), *Cryptobranchus japonicus* and *alleghaniensis* as the only living Amphibia to possess this structure. The neural arch homology of the occipital crest is reaffirmed. The columella stilus of the 32 mm *H. nebulosus* is confluent with the pterygo-quadrate cartilage and because the hyoid and columella have a common blastematous origin in *Hypogeophis* (Marcus 1910), it is suggested that there was an ancestral cartilaginous continuity between the hyoid and pterygo-quadrate cartilage, similar to the commissura terminales of the branchiale. This feature would further emphasize the branchial segmental homologies of the mandibular cartilage, hyoid and branchiale.

The pattern of the cranial nerves is similar to that of other urodele larvae and the arrangement of the profundus and maxillaris nerves supports the view of the descent of urodeles from porolepiforme crossopterygians (Jarvik 1942).

There is a segmental series of eleven head-pharynx segments, a complete branchial segment including a levator muscle, nerve, cartilage bar and gill cleft. Each post-hyoid segment is complete except for the absence of branchiale V and VI, and behind the fourth functional gill cleft there are three vestigial blind ones and then the larynx and trachea leading to the lungs. The masseter (2nd segment), digastricus (3rd segment), dilator laryngeus (10th segment) and trapezius (11th segment) are considered to be the homologues of the other six intervening levator gill arch muscles. The arytenoid and tracheal cartilages are considered to be branchial bars of the 10th and 11th segments respectively, and the lungs to have developed from gill pouches of the 11th segment which failed to reach the exterior early in vertebrate evolution. The classical view of the homology of the laryngo-tracheal skeleton with a branchial bar enunciated by Gegenbaur and Wilder independently in 1892 is therefore upheld; disagreement is merely a numerical one.

The basic segmental components of the amphibian head and pharynx are modified in ontogeny by omission, distortion or addition, in order to fit the animal for a terrestrial existence.

INTRODUCTION

The concept of the segmental organization of the vertebrate head is well established. During the evolution of jawed air-breathing forms from their aquatic jawless ancestors, the various serially homologous segmental components of the head and pharynx were modified or omitted, and new structures developed *pari passu*. Because they develop from fish-like larvae into land-inhabiting air-breathing forms, the urodeles are extremely useful for a study of ontogenetic changes in the segmental components of the head and pharynx. The study should provide in miniature some ideas of the course of phylogenetic development from life in water to that on land.

In a previous investigation on the development of the head of *Cryptobranchus* larvae (Fox 1954), the branchial region was found to be composed of a series of eight homologous branchial arches innervated by nerve IX and vagus 1 to 7 respectively. Each arch included a separate muscle, nerve, gill bar and in front a gill slit (though the posterior ones were vestigial in composition). The dilator laryngeus and trapezius muscles were considered to be the homologues of levators VII and VIII, and the lungs modified gill pouches which had failed to break through to the exterior. *Cryptobranchus* is a primitive urodele and the larva shows many primitive features in its ontogeny. Recently the head of the larval *Hynobius nebulosus* was shown to possess certain features equally primitive (Fox 1957). The occipital crest contained a hypoglossal (spino-occipital) foramen through which emerged a hypoglossal (spino-occipital) nerve; the latter possessed a dorsal and ventral root and a ganglion, and is in fact a typical spinal nerve which emerged between the pre-occipital and occipital arches. These arches are thus of neural origin as Stohr (1882) earlier recognized. The Hynobiidae are considered to be the most primitive living urodeles known (Dunn 1923; Noble 1927, 1931; Pope 1931). Study of the development of the head of *Hynobius* lends support to the view of its primitive nature, and an analysis of its segmentally homologous head components should reveal them in a form as simple as we are likely to find among air-breathing tetrapods (with the possible exception of the Gymnophiona), together with a retention of more numerous vestigial elements than would normally be the case in more specialized types.

The results show in essence an almost complete confirmation of the general conclusions reached from a study of the *Cryptobranchus* head, with some additional features of phylogenetic interest.

Taxonomy and geographical distribution of *Hynobius*

Salamandra nebulosa (Schlegel 1838) is the type species of the genus *Hynobius* of Tschudi (1838). According to Dunn (1923) sixteen species can be placed in the genus, and at least six more have been described since, although the status of some of them is not clear. Dunn, who reviews the taxonomy, considers that the genera *Pseudosalamandra* (Tschudi 1838) and *Salamandrella* (Dybowski 1870) should not be separated from *Hynobius*. *Pseudosalamandra* has as its genotype *Salamandra naevia* (Schlegel 1838), and there is general agreement that this species and *Hynobius nebulosus* are congeneric. *Salamandrella*, which has *Salamandrella keyserlingii* (Dybowski 1870) as genotype has, on the other hand, recently been considered to be generically distinct by Mikamo (1955).

The species of the genus are found from the Urals to Kamchatka, Manchuria, Korea, Sakhalin, the Kuriles and islands of Japan, Formosa and China. *Salamandra* (*Hynobius*) *nebulosa* was first found at Mount Nikajama near Nagasaki, Japan, and many individuals were first brought to Europe by Siebold and Burger (Temminck & Schlegel 1838). The adult *Hynobius nebulosus*, which is widely spread throughout Japan (Tago 1931) and is purely aquatic (Schlegel 1838), is yellowish or dark brown with brown spots, the lateral and ventral surfaces lighter. The sides of the tail are almost black and spotted; a brownish dorsal and ventral yellow stripe extends to the tail. Its length varies between 8·8 and 12·5 cm (Tago 1931).

Previous investigations on the head of *Hynobius*

(a) Adults

The adult bony skull of *Salamandra naevia* (*s.H. naevius*) is first figured in *Fauna Japonica* (Temminck & Schlegel 1838). The skull and hyobranchial skeleton of *H. naevius* was first described in detail by Wiedersheim (1877), and then Drüner (1904) supplemented existing knowledge by describing the hyobranchial skeleton, muscles, 'Kehlkopf Nerven' and anterior spinal nerves. Later on Okajima (1911a) investigated certain aspects of the internal otic foramina in what he believed to be *H. nebulosus*, although Dunn (1923) subsequently considered the species to be *H. vanderburghi*. The skull of *H. leechii* was considered among other urodeles with reference to the sound transmitting apparatus (Dunn 1922) and the septomaxillary bone (Lapage 1928); the structure of the nasal capsule was described for various *Hynobius* species by Chung (1929, 1931) and Chung & Yatabe (1931). The ossifications of the head of *H. retardatus*, *lichenatus* and *nigrescens* were described by Inukai (1932), and by Sato (1941) who figures the skulls of the Formosan *H. sonani* and *formosanus*. The urodele suspensorium, including that of *H. tsuensis*, was considered by de Villiers (1936); more recently Hilton (1946, 1947) described the skull and hyobranchial skeleton of the adult *H. leechii*. The musculature of some members of the Hynobiidae has been studied by various workers and compared with that of other urodeles. The adult head myology investigated includes: the trigeminal of *H. nebulosus* (Luther 1914), opercularis of *H. leechii* (Dunn 1941), and the general musculature (Eaton 1936a).

(b) Larvae

Okajima (1911b) studied the development of the auditory capsule and related structures in early larval stages of *H. nebulosus* (=*H. vanderburghi*, *vide supra*). Important papers by

Edgeworth (1920, 1923 a, b, 1925) on *H. nebulosus* and other larval urodeles dealt with the structure and development of the urobranchiale, laryngeal and hypobranchial musculature, chondrocranium, hyobranchial skeleton and its musculature, and autostyly. Later (1935) he published a comprehensive account including *Hynobius* of the origin and development of the head musculature in amphibia.

The development of the nasal capsule with particular reference to the nasale bone was described in *H. leechii* and *nebulosus* (Chung 1929), with a general study of the nasal region in *H. leechii* alone (Chung 1932). The ductus naso-lachrymalis in the adult was described for various members of the Hynobiidae, and the larval development of the duct in *H. leechii* (Yatabe 1931). The larval hyobranchial skeleton has been investigated by several workers other than Edgeworth. These include 35 mm and 45 mm specimens as well as the adult of *H. keyserlingii* (Bogoljubsky 1925); a series of *H. nebulosus* from 11·5 mm to 100 mm (Tsusaki 1922) and a series from 11 mm to the full grown animal in *H. leechii* (Matumoto 1932). Other investigations on *H. nebulosus* include the development of the lower jaw (Stadtmüller 1929a, 1937), sclerotic cartilages (Okajima & Tsusaki 1921; Stadtmüller 1929b), brain (Sumi 1926), and the occipital crest and anterior spinal nerves (Fox 1957). The development of the balancer has been described in *H. fuscus* (Murayama 1928) and *H. nebulosus* (Oyama 1930b), and recently, the external gill filament blood system and aspects of the head musculature have been described in the larval *H. keyserlingii* by Schmalhausen (1954, 1955). Finally, a description has been given of early cleavage to the formation of the medullary plate in *H. nebulosus* (Kunitomo 1910, 1911); presumptive fate maps of gastrula and neurula stages by vital staining in *H. tokyoensis* (Suzuki & Kobayashi 1939); general embryological development in *H. naevius* (Oyama 1930a), and various Japanese hynobids (Tago 1931).

MATERIAL AND METHODS

The five larvae of *H. nebulosus* to be described were those which originally formed part of a collection of the late Professor J. P. Hill, F.R.S. at University College London, and were previously used to investigate the occipito-spinal region (Fox 1957). The total lengths were 11·5, 14, 17, 22 and 32 mm. Nose-to-cloacal lengths were 6·3, 7·0, 7·6, 10·2 and 14·4 mm respectively. All the larvae were preserved in Zenker's fluid, blocked in paraffin wax, sectioned transversely at 10 μ and stained with Erhlich's haematoxylin and eosin. The graphical technique for reconstruction from dorsal, ventral and lateral viewpoints was the same as that used in an earlier investigation on *Cryptobranchus japonicus* (Fox 1954).

Other larvae which were used in the investigation, and similarly prepared, included 28 and 33 mm specimens of *Eurycea bislineata* from Glen Helen, Yellow Springs, Greene Co., Ohio, received from Dr W. E. Duellman of the University of Michigan; 27 and 37 mm specimens of *Hynobius retardatus* from Kashiro Province, East Hokkaido, received from Dr Kazuya Mikamo of Hokkaido University, Japan; and larvae of *Cryptobranchus japonicus* and *alleghaniensis* in my possession.

THE 11·5 MM STAGE LARVA

The length of the head from the tip of the snout to spinal nerve I is about 2·0 mm. There is no cartilage, but procartilage is present in the quadrate and hyobranchial regions. The nasal sacs each possess a small cavity leading to the exterior, but no internal nares are

developed. The eyes are simple and the lens contains a cavity; the optic nerve is solid. The auditory sacs are as yet simple cellular vesicles. There is no mouth opening to the exterior and the mouth cavity is reduced behind to disappear finally in the yolk mass at a level between spinal nerves III and IV. The incipient gill slits do not open to the exterior, and though the hyoid plug reaches the surface of the head it likewise fails to break through. A small balancer, approximately 0·52 mm long, is present on one side—the other one was certainly lost by damage—and rudimentary gill filaments and forelimb blastemata, but no signs of hindlimbs, are recognizable.

The ectoderm, brain and cranial ganglia are almost free from yolk, but the endoderm and musculature still contain an abundance. Rudimentary eye muscles of yolky mesoderm lie mesial and mesio-ventral to the eyes. The trigeminal musculature arises in the region dorso-posterior to the eye to lead back beneath the gasserian ganglion, and the facial musculature extends from the ventral region of the auditory sac to behind the hyoid pouch.

The ophthalmicus-profundus ganglion is closely associated with the gasserian, but a faint demarcation can be discovered demonstrating that at this stage the trigeminus ganglion is composed of two separate ganglia. The anterior portion of the ophthalmicus-profundus leads forwards mesial to the eye, and dips down to end at its anterior edge over the nasal sac. The gasserian ganglion gives rise to a rudimentary r. mandibularis V, which leads outwards over the quadrate cartilage anlage and trigeminus musculature, and an incipient r. maxillaris V is recognized. The facialis ganglion is situated in its customary position separate from and behind the trigeminus, mesial to the auditory sac. A lateralis VII ganglion lies dorsal to, though fused with the geniculate portion. The r. buccalis facialis leads antero-ventrally, lateral to the trigeminus musculature and close to the skin neuromasts, and it was traced latero-ventral to the eye. A small r. superior ophthalmicus facialis could merely be followed to the skin near its origin. The r. hyomandibularis facialis is situated behind the hyoid pouch and no divisions were recognizable. No r. palatinus facialis nor nerves III, IV and VI were discerned. A glossopharyngeal ganglion (about 100 μ long by 160 μ high) is joined to the vagus ganglion dorsally. The latter is considerably longer than the glossopharyngeal ganglion. The early development of nerves IX, vagus I and II and the truncus-intestino-accessorius is recognized, and there is a well developed lateralis superior ramus X. Spinal nerves have been described (Fox 1957); nerves IV and V are generally the same as spinal nerve III.

The vena capitis medialis (embryonic anterior cardinal vein, Goodrich 1930) directed anteriorly from the ductus Cuvieri, lies mesial to ganglia IX and X and the auditory sac, lateral to the occipital somites and above the aortic vessels. It receives posterior and middle cerebral veins from the regions mesial to the vagus and auditory sac, and collects blood from a dorsal division mesial to the eye and a ventral one below the optic nerve. The vessels join below the trigeminus ganglion. The ductus Cuvieri also receives a vessel from below the anterior ventral aortic arch, which runs backwards close to the heart. Behind, the pronephros is surrounded by the large posterior cardinal sinus.

Three ventral aortae lead latero-dorsally from the upper region of the heart (afferent epibranchial arteries). These correspond but do not fuse with three efferent epibranchial arteries (from the lateral dorsal aorta) in the gill region; the third efferent epibranchial artery further divides into two (aortic arteries III–VI). Further forwards the hyoid artery

(efferent epibranchial II) joins the lateral dorsal aorta. In front of the hyoid artery the lateral dorsal aorta continues forwards as the internal carotid, above the roof of the mouth, lateral and close to the hypophysis and latero-ventral to the forebrain; it ends on the ventro-lateral surface as an arterial plexus. Behind, the lateral dorsal aortae of each side join beneath the notochord at about the level of spinal nerve I (figure 1).
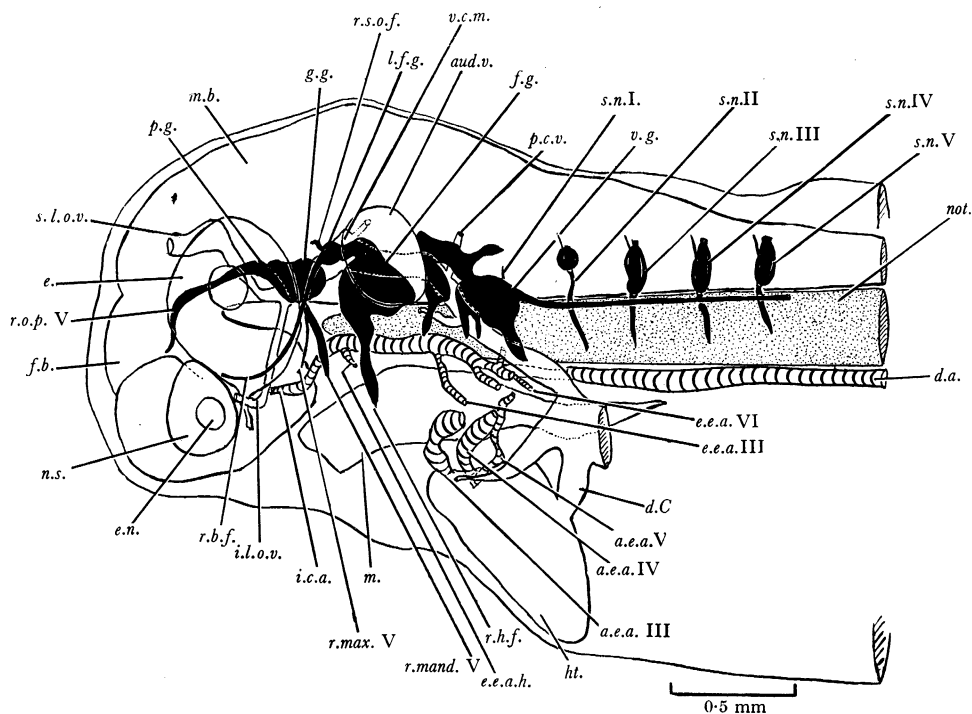

FIGURE 1. 11·5 mm stage *H. nebulosus*. Lateral reconstruction of the head and pharynx.

THE DEVELOPMENTAL PATTERN OF THE HEAD AND PHARYNX OF *H. NEBULOSUS* FROM THE 14 MM TO THE 32 MM STAGE LARVA

(1) *The balancer and early limb development*

In the 14 mm stage the balancer is about 1·12 mm and the forelimb 1·03 mm long; hindlimb blastemata are already apparent, although Low (1927) reported the first trace of the latter in a 16·5 mm specimen. No balancer is recognizable from the 17 mm stage onwards. Here the trifid forelimbs and undivided hindlimbs are 1·04 and 0·60 mm long respectively. A beginning of the fourth digit is apparent in the forelimb of the 22 mm specimen which is now 1·97 mm long; the undivided hindlimb is 1·0 mm long. The 32 mm stage has well developed fore- and hindlimbs, the former 3·15 mm long bearing 4 digits, the latter now possesses 5 digits. The results tend to agree with those of Oyama (1930 b) in *H. nebulosus*, who found that embryos which normally hatch 3 weeks after being spawned were 12 to 13 mm long, and possessed a balancer and forelimbs (on each side) 1·25 and 1·0 mm long respectively. About 2 weeks after hatching—10 days in *H. naevius* (Murayama 1928)—the balancer is lost. *H. nebulosus* (stage 32 to 33 Glaesner) 11 to 12 mm long has paired balancers, 3 pairs of external unbranched gill filaments, and small fore-limb anlagen (Suzuki 1933), as in my 11·5 mm specimen. The presence of a balancer was

also reported in a 13 mm *H. nebulosus* by Okajima (1911 *b*). *H. naevius* hatches 5 weeks after being spawned, and at this time it is considerably larger than *H. nebulosus*, being between 21 and 22 mm long (Oyama 1930 *a*). *H. naevius* also shows rudiments of forelimbs when 15 mm long, 3 weeks after being spawned. Balancers are reported in *H. nebulosus*, *leechii, fuscus* and *cristatus* (Tago 1931), and in the latter rudiments of forelimbs were seen at 15 mm (4 to 6 weeks after spawning). No eyelids are present in these larvae, but they occur in the adults. The time taken for the embryo to hatch depends in part on the atmospheric temperature (Shitkov 1895). The latter worker reported larvae of *H. keyserlingii* to be 10·0 mm with balancers 1·0 mm long on hatching. At 16 mm the hindlimbs
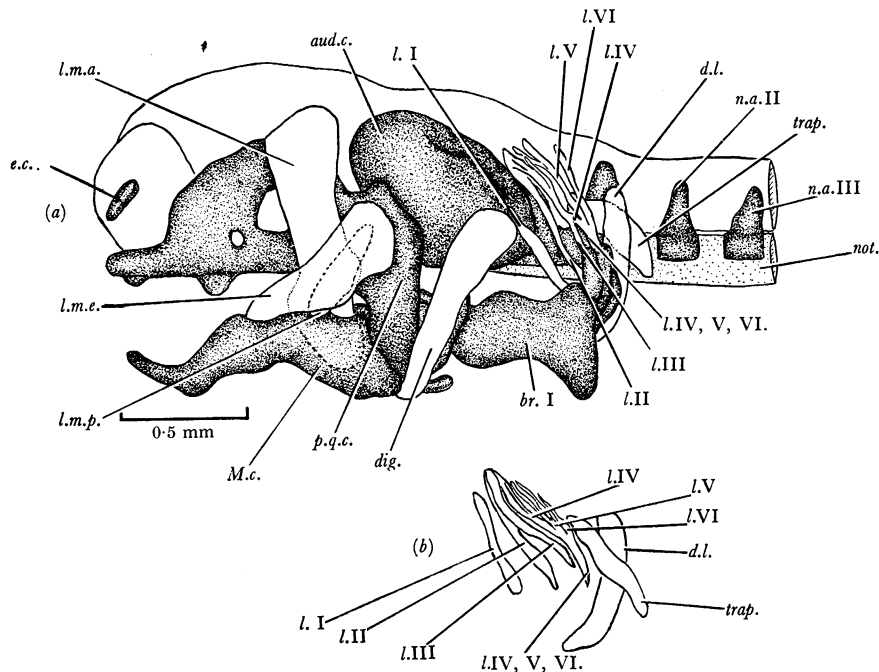

FIGURE 2. 14 mm stage *H. nebulosus*. Lateral reconstruction of the cartilage, jaw and levator musculature. (*a*) left side, (*b*) levators of the right.

were scarcely indicated; the forelimb rudiments were first noticed at 12 to 13 mm (Shitkov 1899). The young larvae of *Hynobius* are like *Ambystoma* in possessing balancers, dorsal fins and long external gill filaments (Noble 1931); the anterior limbs develop before the posterior ones (Noble 1927).

(2) The cartilage

The chondrocranium, hyobranchial skeleton and neural arches are chondrified in the 14 mm stage (figures 34 to 36, plate 5), and there are some incipient ossifications. These skeletogenous structures become progressively larger and more complex as development proceeds. Tsusaki (1922) found an undivided hyoid, ceratobranchiale and hypobranchiale I and II and ceratobranchiale III and IV together with a ventral copula already present in an 11·5 mm *Hynobius nebulosus*. Okajima (1911 *b*) reported however that the chondrification of the branchial skeleton and auditory capsule commences at about 13 mm in the same species. This agrees with Edgeworth's (1920) specimens in which the hyobranchial skeleton was precartilaginous at 12 mm, and chondrification had occurred by the 15 mm

FIGURE 3. 14 mm stage *H. nebulosus*. Ventral reconstruction
of the chondrocranium and anterior vertebrae.

FIGURE 4. 14 mm stage *H. nebulosus*. Lateral reconstruction of the cartilage
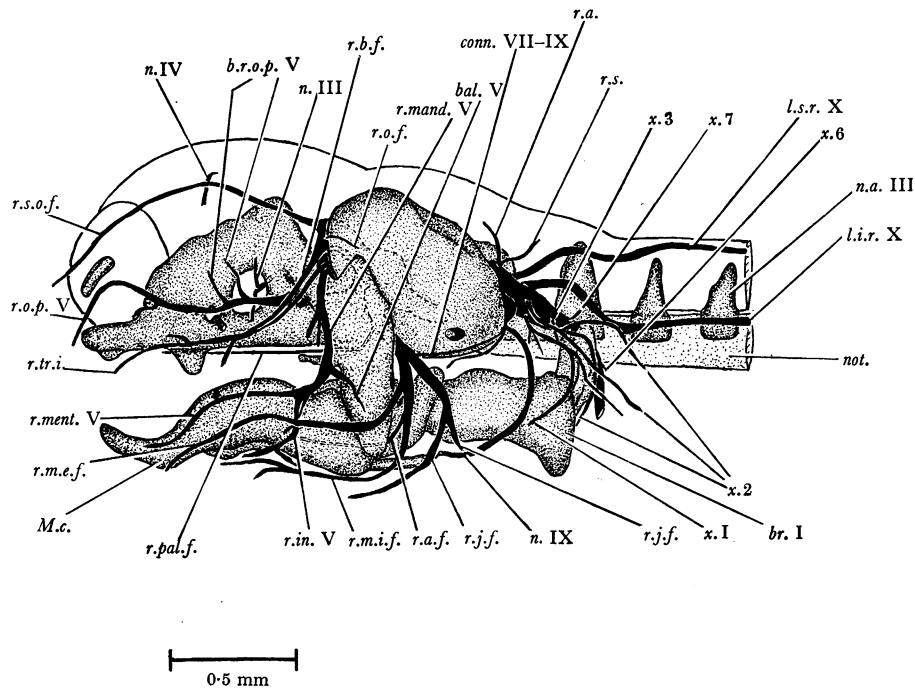and blood system of the head and pharynx. Branchiale are omitted.

FIGURE 5. 14 mm stage *H. nebulosus*. Lateral reconstruction of the cartilage and cranial nerves.
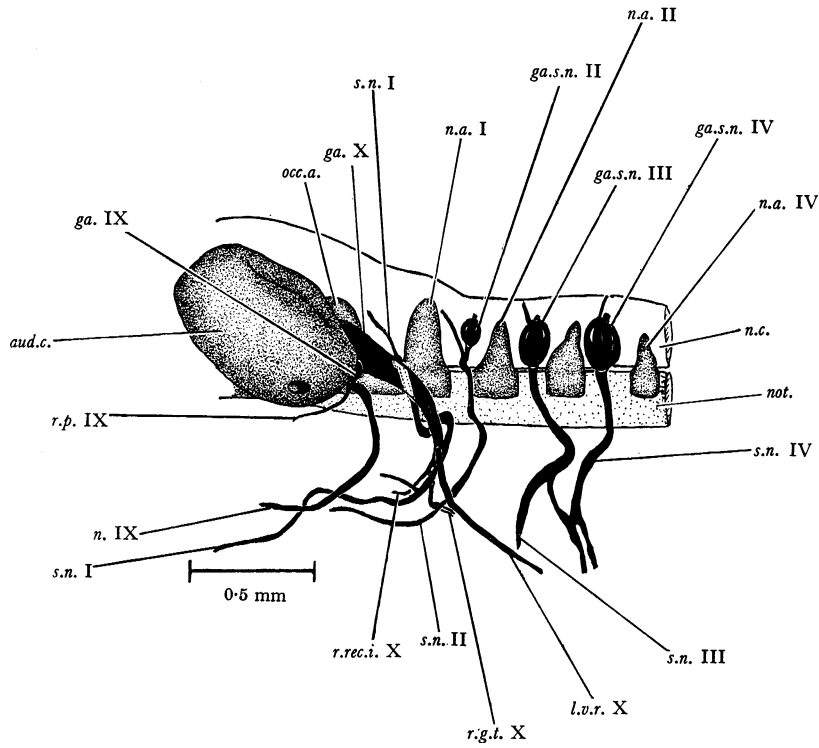

FIGURE 6. 14 mm stage *H. nebulosus*. Lateral reconstruction of the truncus-intestino-accessorius X and anterior spinal nerves.

stage. In *H. leechii* the hyobranchial skeleton anlage is first noted at 11·0 mm, and chondri-
fication has occurred by the 13 mm stage (Matumoto 1932). The anlage of the trabeculae
cranii is discerned in the 10·0 mm larva of *H. leechii*, and it becomes cylindrical with an
incipient lamella around the optic nerve in the 12 mm stage (Chung 1932). The first
chondrifications in the ascending otic and pterygoid processes and in the pterygo-quadrate
cartilage are recognized in *H. nebulosus* at 13 mm. By the 20 mm stage the processus
pterygoideus was found to be confluent with the trabecula and the inner margin of the
antorbital process, and is wholly cartilaginous along its length (Edgeworth 1923 *a*).

The chondrocranium of the 14 mm *H. nebulosus* is about 1·8 mm long and 2·0 mm wide
(at the level of the auditory capsules) (figures 2, 3). In the 32 mm stage it is 3·64 mm long
by 3·92 mm wide; i.e. about double the size (figures 23, 27). Viewed ventrally, a large
hypophysial fenestra, bounded by the trabecular plate anteriorly, the basal plate posteriorly
and the paired trabeculae laterally is present in the 14 mm stage (0·75 mm long and
0·6 mm wide); in the 32 mm stage it is 1·76 mm long and 0·9 mm wide. The length of the
basal plate is 0·66 mm (14 mm stage), and 1·08 mm (32 mm stage). A foramen abducentis
which transmits the abducens nerve VI is not yet present in the 14 mm stage, though
nerve VI is suspected, but the foramen is present in the basal plate in all subsequent stages
(figure 44, plate 6). It is situated at about the level of the tip of the notochord, between
the latter and the auditory capsule in the 17 and 22 mm stages (figures 8, 13), but slightly
further in front of the notochord in the 32 mm specimen (figure 27). The position is the
usual one for urodeles (see Gaupp 1911), and practically identical with that of a 35 mm
Salamandra maculosa (Stadtmüller 1924).

The paired cartilaginous auditory capsules are each joined to the basal plate by a
basicapsular commissure. There is no fusion between the anterior upper capsule surface
and the pila prootica in the 14 and 17 mm stages (figures 2, 7), but a taenia marginalis
posterior sealing off a prootic recess is present in the 22 and 32 mm specimens (figures 12,
23). In the latter the auditory capsule has grown forwards shutting off from external view
the trigemino-facialis ganglion (figures 40, 41, plate 6). The chondrocranium of the
20 mm specimen of *H. nebulosus* figured by Edgeworth (1923 *a*) bears a clear similarity to
my 22 mm specimen in the prootic region. An extremely small foramen ovalis is present
in the ventro-lateral surface of the auditory capsule of the 14 mm stage, but a columella
auris was difficult to distinguish. Its absence in a 20 mm specimen was reported by
Edgeworth (1923 *a*). In later stages the foramen ovalis is larger and at 32 mm it is about
0·36 mm long and 0·40 mm wide, as the name suggests oval in outline. The cylindrical
columella is about 0·34 mm long in the latter specimen, and a stilus leads forwards from

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PLATE 5

Photomicrographs, all transverse sections 10 μ thick of *H. nebulosus*.

FIGURE 34. 14 mm. Pterygo-quadrate cartilage; origin of r. mandibularis V, from trigeminus,
emerging between levator mandibulae posterior and externus.

FIGURE 35. 14 mm. Balancer nerve from r. mandibularis V to balancer.

FIGURE 36. 14 mm. Vestigial gill cleft 5 of the 8th head segment.

FIGURE 37. 17 mm. Origin of vagus branchial nerve V.

FIGURE 38. 17 mm. Origin of vagus branchial nerve VII.
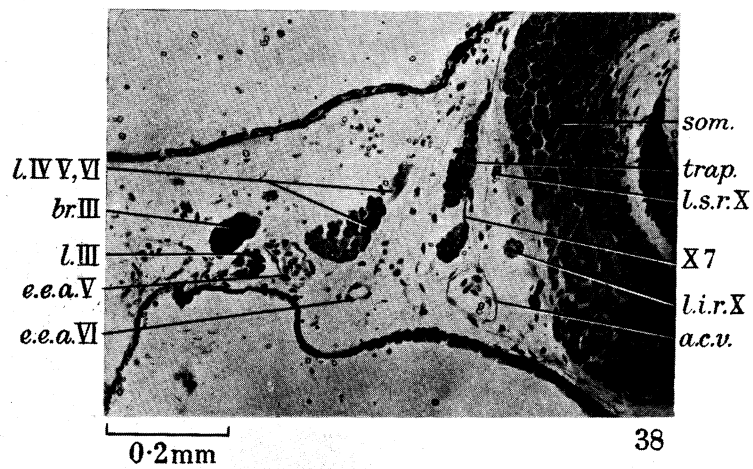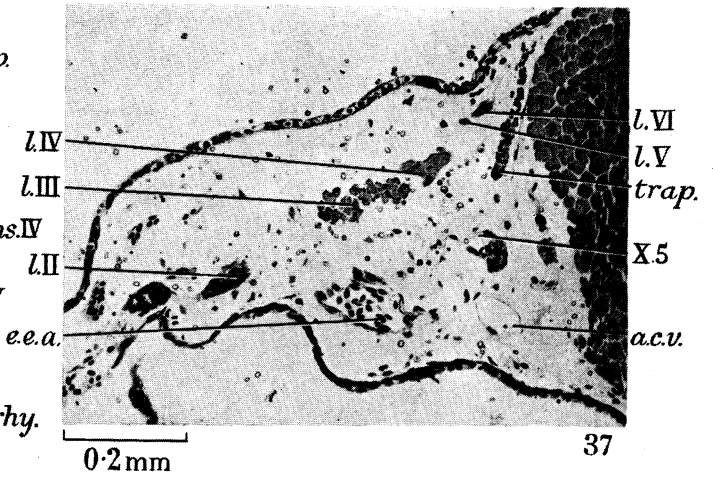
FIGURES 34 TO 38

PLATE 6

Photomicrographs, all transverse sections 10 μ thick of *H. nebulosus.*

FIGURE 39. 14 mm. Origin of vagus branchial nerve VI.
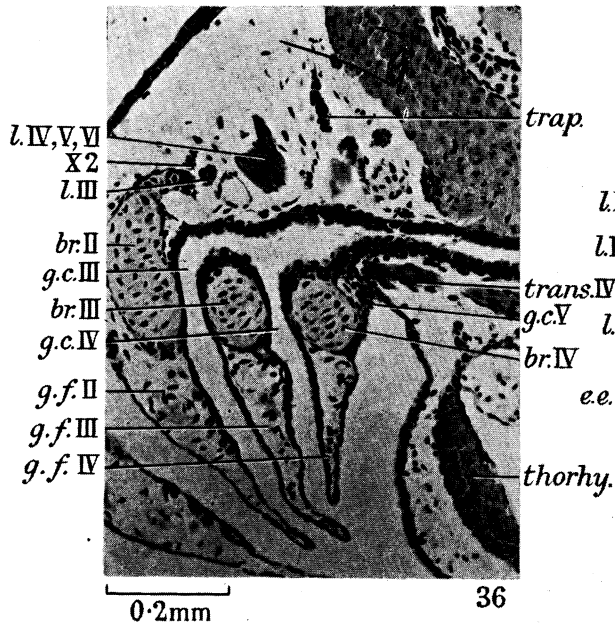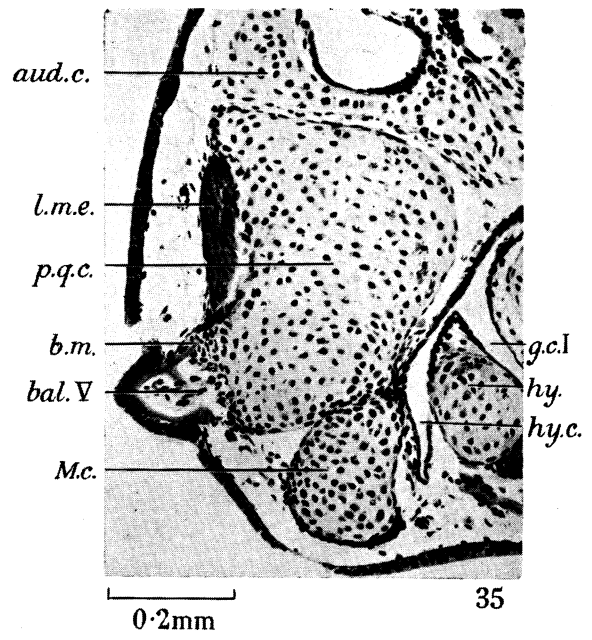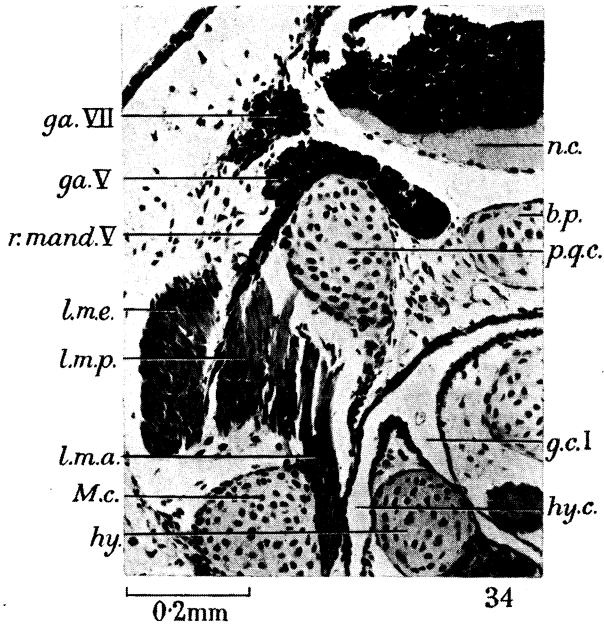
FIGURE 40. 32 mm. Innervation of rectus posterior by nerve VI.

FIGURE 41. 32 mm. Region at the extreme anterior end of the auditory capsule.

FIGURE 42. 32 mm. Syndesmotic joint in basal process.

FIGURE 43. 32 mm. Origin of rami hyomandibularis and palatinus facialis nerves.

FIGURE 44. 32 mm. R. hyomandibularis facialis situated beneath the columella stilus.

FIGURE 45. 32 mm. Posterior origin of columella stilus from columella.

FIGURE 46. 32 mm. Insertion of the r. abducens at the level of the fenestra perilymphatica.

FIGURE 47. 22 mm. Vestigial gill clefts 5 and 6 of the 8th and 9th head segments respectively.

FIGURE 48. 32 mm. Insertion of dilator laryngeus on the arytenoid.

FIGURE 49. 32 mm. Vestigial gill clefts 5 and 6 of the 8th and 9th head segments respectively.

FIGURES 39 TO 49

trap.
d.l.
ga X
li.r.X
X.6
a.c.v.

0·1mm 50

h.b.
ga.IX,X
occ.a.
aud.c.
h.n.
f.hyg.
h.n.
not.

0·2mm 51

l.VI
l.V
X.3
trap.
X.2
ga.X
a.c.v.
e.e.a.IV,V,VI
phx.
g.c.V
cerbr.IV

l.IV
l.III
l.II
e.e.a.III
X.1
l.I
cer.ex.
g.c.I
cerbr.I
g.c.II
cerbr.II
g.c.III
cerbr.III
g.c.IV

1mm 52

d.l.
trap.
e.e.a.VI
l.IV V VI
e.e.a.V
d.l.
g.c.V

comm.t.
e.e.a.IV
l.III
l.II
cerbr.II
e.e.a.III
cerbr.I
g.c.III
cerbr.III
g.c.IV
cerbr.IV
g.f.I
g.f.IV

1mm 53

g.c.V
cerbr.II
g.c.III
cerbr.III
g.c.IV
cerbr.IV

not.
som.
d.a.
g.c.VII
p.ary.
lrx.
trans.IV
cons.arc.
thorhy.

1mm 54

ga.X
p.c.v.
a.c.v.
e.e.a.III
l.d.a.
cerbr.III
g.c.IV

occ.a.
not.
g.c.VII
trans.IV
cerbr.IV
thorhy.
s.n.I,II
cons.arc.

1mm 55

l.V
l.IV
X.3
l.III
l.II
X.1
l.I
g.c.V
g.c.IV
g.c.II
cerbr.IV
cerbr.I
g.f.IV
g.f.I

vert.I
n.c.
not.
g.c.V
cerbr.IV
g.c.IV
g.f.IV
sph.l.
p.ary.
peric.

1mm 56

FIGURES 50 TO 56

it which is in cartilaginous continuity with the posterior upper margin of the pterygo-quadrate cartilage (figure 23; figures 43 to 45, plate 6). No operculum, delimited from the wall of the auditory capsule, is recognized at any stage. A tectum synoticum joins the paired auditory capsules and covers a short length of the hind-brain in the 22 and 32 mm stages (figure 46, plate 6). Platt (1897) considered the tectum synoticum (her tectum interoccipitale) to be formed from paired anlagen in *Necturus*, as dorsal extremities of the occipital arches, similar to the paired anlagen connecting the dorsal extremities of the neural arches. The tectum arises from distinctly paired cartilages which are still independent though adjacent dorsally, in the 22 mm stage *Hynobius*, but at 32 mm no sign of its paired origin is recognizable. Gaupp (1906) found the relationship of the tectum synoticum to the occipital and neural arches not proven.

In the 14 mm stage the oculomotor foramen, bounded in front by the pila metoptica and behind by the pila prootica, is about $160\,\mu$ long; the optic foramen, bounded in front by the pila preoptica is about $70\,\mu$ long. Both foramina are almost circular in outline and undivided at the 17 mm stage, but here the oculomotor foramen is smaller than the optic. In the older specimens the former is divided into an anterior supraorbital foramen for the supraorbital artery, and a posterior one which subserves for the emergence of the oculomotor nerve (figures 12, 23). The optic foramen is undivided in all stages and transmits the optic nerve and the optic vein.

The first sign of sclerotic cartilage is on the right side of the 14 mm stage, where a tiny cartilaginous nodule, 30 to $40\,\mu$ long, is found in the dorso-mesial region of the fibrous connective tissue surrounding the eye. This isolated cartilage is larger and present on both sides in the 17 mm stage, and on the right there is a trace of a ventro-mesial cartilage. There are paired upper and a large ventral sclerotic cartilage on both sides in the 22 mm animal and these fuse together to form an incomplete ring, deficient posteriorly, in the 32 mm specimen (figure 23). Okajima & Tsusaki (1921) found no trace of sclerotic cartilage in an 18 mm *H. nebulosus*, but an interrupted cartilaginous ring was recognized at 24·5 mm. There was no sign of sclerotic cartilage in a 15 mm *H. leechii*, but 10 days later in a 20 mm stage cartilage was found with the rectus inferior muscle inserted upon it (Yatabe 1932). Four-fifths of the sclerotic ring was present by the 30 mm stage. The results in this present work demonstrate that the sclerotic cartilage in *H. nebulosus* originates earlier than has hitherto been believed. The sclerotic ring is greatly reduced in the

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PLATE 7

Photomicrographs, all transverse sections $10\,\mu$ thick of *H. nebulosus* and *retardatus*.

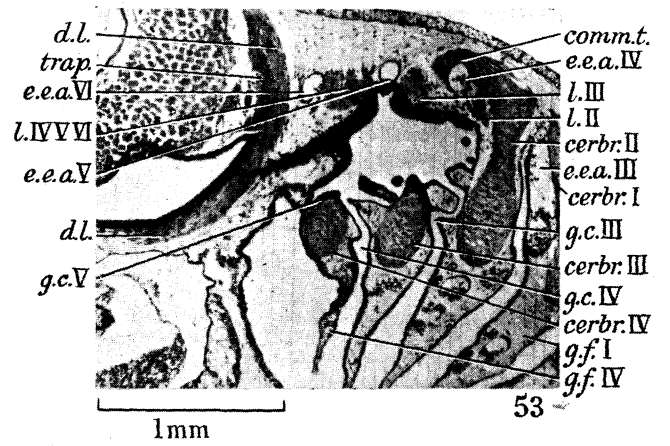FIGURE 50. 22 mm. *H. nebulosus*. Origin of vagus branchial nerve VI.

FIGURE 51. 37 mm. *H. retardatus*. Hypoglossal foramen and nerve of left side.

FIGURE 52. 37 mm. *H. retardatus*. Levator a. branchialis musculature of I–VI, and vestigial gill cleft V.

FIGURE 53. 37 mm. *H. retardatus*. Vestigial gill cleft V (8th head segment).

FIGURE 54. 37 mm. *H. retardatus*. Vestigial gill clefts V and VII, of head segments 8 and 10, and arytenoid cartilages.

FIGURE 55. 32 mm. *H. nebulosus*. Vestigial gill cleft VII (10th head segment).

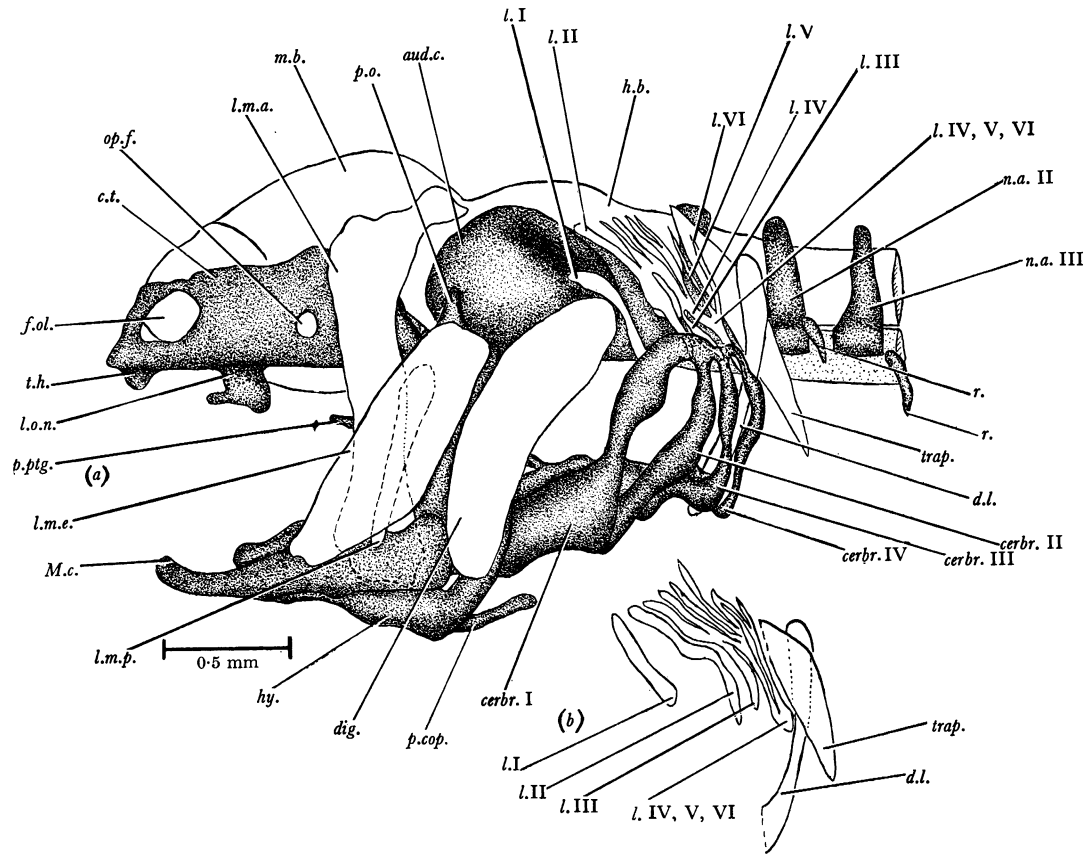FIGURE 56. 27 mm. *H. retardatus* Vestigial gill cleft V and arytenoid cartilages.

FIGURE 7. 17 mm stage *H. nebulosus*. Lateral reconstruction of the cartilage, jaw and levator
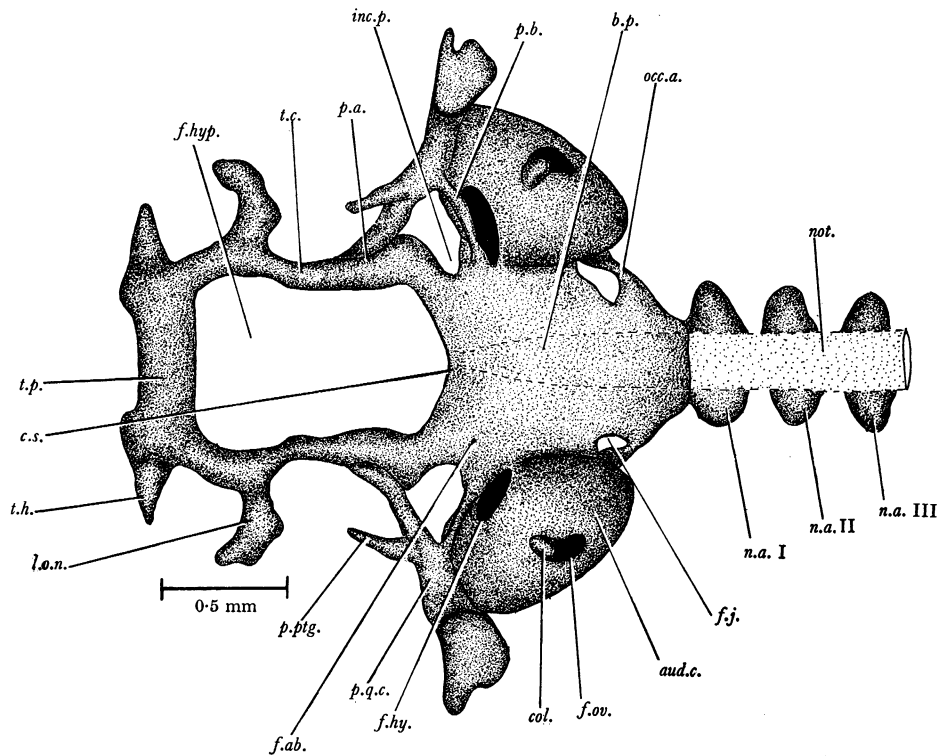musculature. (*a*) left side; (*b*) levators of the right.

FIGURE 8. 17 mm stage *H. nebulosus*. Ventral reconstruction of the
chondrocranium and anterior vertebrae.

metamorphosed form (Stadtmüller 1929 b). Its function is to maintain the eye in constant shape and provide a surface for the attachment of the extrinsic eye muscles (De Beer 1937).

In the nasal region of the 14 mm stage a small anterior cornu trabecula, and behind the lamina orbito-nasalis (planum antorbitale) are situated below the nasal sac. Dorso-mesial to the latter is the ethmoidal column (Terry 1906; Higgins 1920) (figures 2, 4). There is as yet no complete foramen olfactorius. These cartilage structures, together with the trabecular plate, are larger and more substantially developed in the 17 mm form, and there is a complete foramen olfactorius (figures 7, 8, 16). The latter is not completely closed in a 15 mm *H. leechii*, but closure was recognized at 20 mm (Chung 1932). The nasal sac is partially roofed by the planum tectale in the 22 mm stage, and there is some cartilaginous backgrowth from the lamina orbito-nasalis towards the anterior end of the processus pterygoideus. The nasal capsules are separate from one another (figures 12, 13, 17). In the 32 mm form a dorsal tectum internasale transversely joins the capsules (figure 18), and in front the tectum meets the anterior end of the trabecular plate to form the front wall of the cavum internasale, which lodges the anterior part of the olfactory lobes. In the 22 mm specimen merely a procartilaginous tectum internasale is recognized. At 32 mm further development of the capsule has formed a dorso-lateral fenestra narina, a ventral fenestra choanalis (f. basalis), a posterior fenestra orbito-nasalis (between the orbit and the nasal capsule) and a partially developed fenestra lateralis nasi (s.f. infra conchalis). Inside the nasal capsule, in the mesial wall, are a posterior upper fenestra apicale, and an extremely small anterior one. The fenestra olfactorius is unchanged (figures 18, 23). The lamina orbito-nasalis has grown forwards and has begun to form the outer floor of the capsule, to enclose the fenestra choanalis. There is still no complete connexion between the cornu trabecula and the lamina to form the floor of the capsule (lamina transversalis anterior), nor is there a lateral cartilago ectochoanalis. The cartilago obliqua forms the medial border of the fenestra narina, and the cartilago retronarina separates the foramina narina and lateralis (Stadtmüller 1936). At this 32 mm stage no fenestra dorsalis nasi has developed; the latter is a secondary formation and develops late in larval life, by regression of cartilage of the capsule roof (Jarvik 1942). The fenestra dorsalis is found just before metamorphosis in *H. leechii* (Chung 1932); it is very broad in the adult *H. nebulosus* (Chung 1931). A fenestra apicale is mentioned for the first time during the development of *H. leechii* just before metamorphosis (Chung 1932); Chung (1931) states that the fenestra lateralis (his f. retronarina) is wholly lost in *H. nebulosus* and *Onycho-dactylus fischeri*. It is present in *H. leechii*, in continuity with the incisura ectochoanalis just before metamorphosis, and in the adult *H. tsushimensis* and *Pseudosalamandra* (Chung 1931, 1932). A fenestra lateralis would seem to be present, but not sealed off ventrally during the ontogeny of *H. nebulosus* in my series.

Internal nares are present in the 14 mm stage and onwards; Okajima (1911 b) reported them in a 13 mm specimen of the same species.

Behind the auditory capsules is the (paired) segmental occipital crest (Goodrich 1911) of neural origin (Fox 1957). At 14 mm it is short in length and the dorso-anterior part is not fused with the mesio-posterior surface of the auditory capsule. Its segmental relation-ship with the neural arches is demonstrated (see figure 3). The occipital crest fuses with the mesio-posterior surface of the auditory capsule at 17 mm delimiting a foramen jugularis

which subserves for the emergence from the chondrocranium of ganglia IX and X (figures 8, 10). The foramen jugularis is not visible from the lateral viewpoint; it is situated between the post-auditory capsule and the occipital crest. The arrangement is similar in older stages. There is no hypoglossal foramen in the 14 mm specimen; it is suspected as a faint cleft on the right side at 17 mm, but it is clearly present on both sides in the 22 and 32 mm stages. The occipital crest is 0·16 mm long and 0·30 mm high (14 mm) and about 0·34 mm by 0·8 mm in the 32 mm stage.

FIGURE 9. 17 mm stage *H. nebulosus*. Lateral reconstruction of the cartilage and blood system of the head and pharynx. Branchiale behind the hyoid are omitted.

Each neural arch, present in the 14 mm stage, meets its fellow of the other side over the nerve cord in the 17 mm and later stages. Lateral dorsal cartilaginous connexions are present between the first four neural arches, on each side, in the 22 mm stage (figure 12); the more posterior neural arches were not considered. In the 32 mm specimen neural arches 2 and 3 each possess a cartilaginous neural spine, and a prezygapophysis and posterior zygapophysis on each side. A joint is recognized between the posterior and prezygapophyses of the 2nd and 3rd neural arches. Neural arch I is incomplete on the left side but cartilaginously complete on the other. The upper portion is little differentiated but there is a distinct joint between the posterior end and the prezygapophysis of the second arch (figure 23). There is no recognizable occipito-vertebral joint at any stage. A distinct trace

FIGURE 10. 17 mm stage *H. nebulosus*. Lateral reconstruction of the cartilage and cranial nerves.

FIGURE 11. 17 mm stage *H. nebulosus*. Lateral reconstruction of the truncus-intestino-accessorius X and anterior spinal nerves.

of paired occipital condyles is recognized in the 22 mm form; these are more pronounced in the 32 mm specimen. The 2nd and 3rd vertebrae of the 17 and 22 mm stages each possess small paired vestigial ribs, not joined to them (figures 7, 12). The ribs are larger in the 22 mm stage. At 32 mm vertebra I has a tiny cartilaginous nodule on each side fused against the base of the neural arch (vestigial rib), the 2nd and 3rd vertebrae each have a pair of large ribs (figure 27), with a cartilaginous tubercular connexion to the neural arch, and a smaller ossified capitular union with the centrum (see Gray 1930).

The anatomical relationship of the facialis-auditory ganglion to the medial auditory capsule fenestrae in the larval series, reveals the developmental pattern of these fenestrae (figures 19–22). At 14 mm there is merely a large oval-shaped opening into the
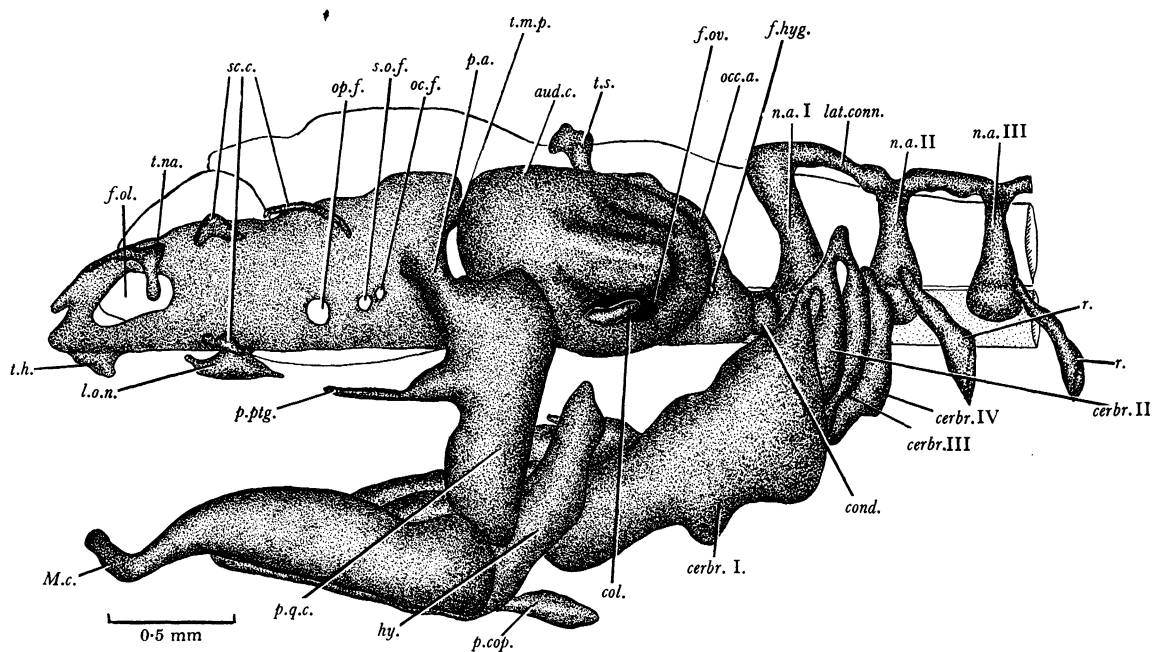

FIGURE 12. 22 mm stage *H. nebulosus*. Lateral reconstruction of the chondrocranium, jaws and hyobranchial skeleton, anterior vertebrae and ribs.

capsule. The 'facialis-auditory' ganglion is situated mesial to this aperture, and its posterior portion projects inside the capsule. At 17 mm the single fenestra has divided into an upper fenestra endolymphatica, an anterior ventral fenestra acoustica and a posterior ventral fenestra perilymphatica. Separation of the upper from the two lower fenestrae is the result of cartilaginous formation lateral to the ganglia. Separation of the two lower ones is the result of cartilaginous growth mesial to the ganglia. Furthermore, in the 17 mm stage there is a prefacial commissure mesial to the r. hyomandibularis facialis, so that the latter appears to emerge from the auditory capsule cavity, through the fenestra acoustica. This is not so. The r. hyomandibularis facialis leads to the exterior through a short passage, bounded laterally by the medial wall of the auditory capsule and bounded mesially by the prefacial commissure. The condition is similar in the 22 mm stage, except that the fenestra endolymphatica has lengthened, and that 140 μ in front of the fenestra acoustica there is another extremely small round fenestra about 15 μ in diameter. The 32 mm stage possesses a fenestra endolymphatica dorsalis and ventralis on one side (it is

undivided on the other), a fenestra acoustica anterior and posterior, and a single fenestra perilymphatica. The prefacial-auditory canal has lengthened and the tiny anterior fenestra is now 480 μ in front of the fenestra acoustica anterior, demonstrating the forward growth of the auditory capsule during development. An 80 mm *Cryptobranchus japonicus* possessed in addition to an upper fenestra endolymphatica, three fenestrae acousticae and a single fenestra perilymphatica (Miyawaki 1929). The small anterior fenestra of *Hynobius* may possibly be the fenestra acoustica anterior; if so, then the two others would be acoustica medius and posterior respectively (Fox 1954, p. 259). The adult *H. nebulosus* possesses two perilymphatic fenestrae, and only a single one in the larva (Okajima 1911 a).
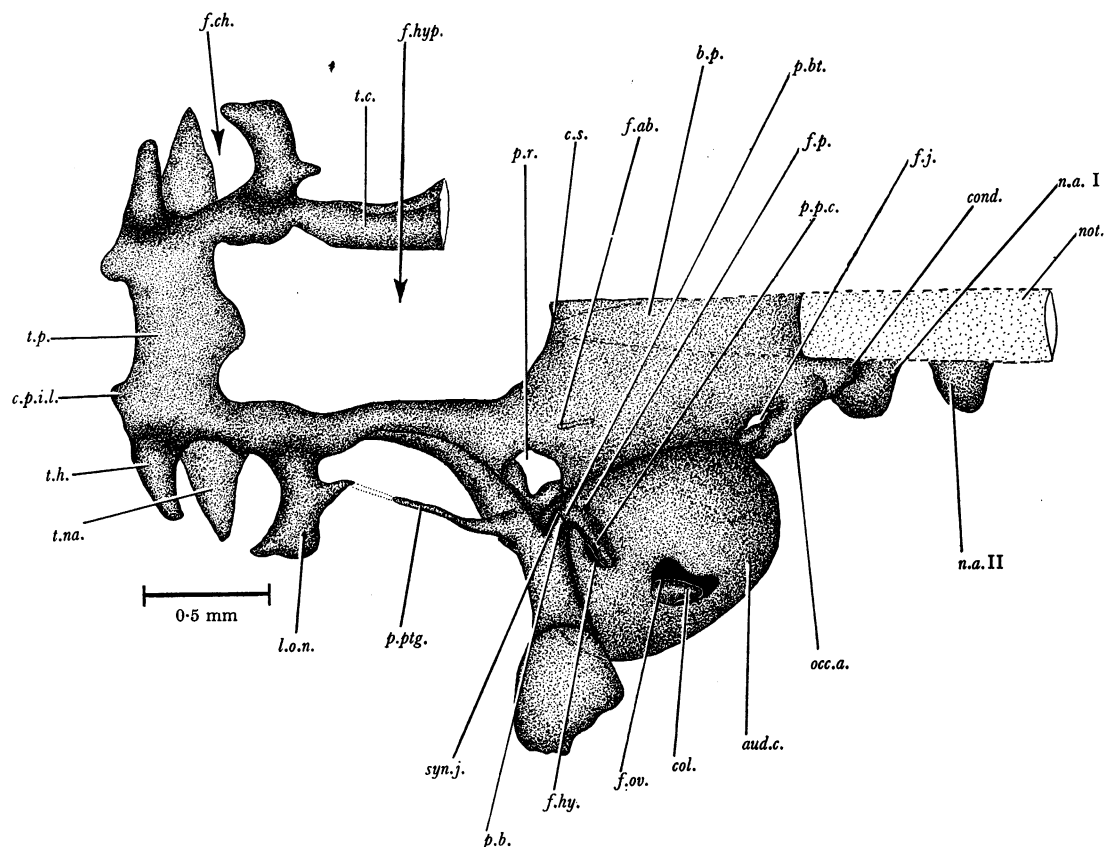

FIGURE 13. 22 mm stage *H. nebulosus*. Ventral reconstruction of part of the chondrocranium and anterior vertebrae.

The pterygo-quadrate cartilage in the 14 mm stage possesses a processus ascendens confluent with the pila prootica, and a processus oticus fused with the anterior external surface of the auditory capsule. They are present and well developed in all subsequent stages. A short cartilaginous processus pterygoideus extends forwards for about 0·18 mm, and continues in front as a stream of unchondrified cells, which leads to the trabecula just behind the lamina orbito-nasalis. In the 17 mm stage the chondrified processus pterygoideus is 0·34 mm long but it does not reach either the trabecula or the lamina. A processus basalis is now recognized, which extends from the quadrate cartilage to the basal plate, over the antero-ventral surface of the auditory capsule (figure 8). At 22 mm the processus pterygoideus extends forwards 0·5 mm; a thread of unchondrified cells (situated over the pterygoid ossification) extending for about 160 μ joins the tip of the process to

a cartilaginous backgrowth of the lamina orbito-nasalis. A faint cleft is recognized in
the basal connexion which may separate a processus basalis from the basitrabecularis
(figure 13). The condition is called semistreptostylic by Gaupp, and the autostylic sus-
pension is incomplete (de Beer 1937). A syndesmotic joint is developed in the basal ridge
in *Plethodon* (49 mm), *Salamandrella* (34 mm), and *Ranodon* (85 mm) (Edgeworth 1925),
and in a 37 mm *Hynobius nebulosus* (Edgeworth 1923 a). Whether the joint is a primitive
phylogenetic feature (Luther 1914), or a secondarily acquired one (Edgeworth 1925) has
still to be resolved. A post-palatine commissure is recognizable in the 22 mm form, which
separates the rami hyomandibularis and palatinus facialis, as these emerge from the
chondrocranium. The palatine nerve thus emerges through its own palatine foramen at a
level slightly postero-lateral to the foramen abducentis (figure 13). In the 32 mm stage the
processus pterygoideus is 0·88 mm long and ends freely (figure 40, plate 6). No carti-
laginous ethmoidal fusion between the pterygoid cartilage and either the trabecula or
lamina orbito-nasalis was recognized in this particular series of *H. nebulosus*. The results do
not confirm those of Edgeworth (1923a, 1935), who described the pterygoid process
wholly chondrified and confluent with the trabecula and the inner surface of the antor-
bital process in a 20 mm larva of the same species; the anterior portion disappeared by
the 37 mm stage. The basitrabecularis and basal processes, together with the syndesmotic
joint, and the post-palatine commissure are similar but larger in the 32 mm form (figure
27; figures 42 to 44, plate 6).

From 14 mm onwards (paired) Meckel's cartilage, hyoid and branchial arches are
developed (figures 30–33). Previous workers agree on the presence of these structures.
The hyoid and branchiale embrace and support the pharynx. Meckel's cartilage
fuses with its partner at the anterior symphysis and leads behind to hinge against
the mesio-ventral surface of the quadrate cartilage. The hyoid, joined ventro-anteriorly
to the front of the copula ends freely dorso-posteriorly. It is divided into an upper cerato-
hyale and lower hypohyale in the 22 mm stage (figure 32), but undivided in the 17 mm
form (figure 31). Behind the hyoid, ceratobranchiale and hypobranchiale I, II and III
are already delimited in the 14 mm stage. Hypobranchiale III is extremely small and
clear demarcation from the fused lower ends of ceratobranchiale III and IV is only
apparent from about 17 mm onwards. Ceratobranchiale IV only is recognized in all
stages. The four ceratobranchiale are connected dorsally by commissura terminales.
A branchial plate is recognized (first described for *Triturus cristatus* by Gaupp 1906, p. 705),
in contrast to *Cryptobranchus* larvae which do not possess one (Smith 1920; Fox 1954).
Smith described a branchial plate in the Plethodontidae, Salamandridae and Amby-
stomidae. It is figured in a 30 mm larval branchial skeleton (Edgeworth 1923 b) and
suggested in a 19 mm specimen of *H. nebulosus* (Tsusaki 1922), but not shown in *H. leechii*
(Matumoto 1932), or in *H. keyserlingii* (Bogoljubsky 1925). The ventral cylindrical copula
ending behind as a dorso-ventrally flattened plate is 0·48 mm long at 14 mm and about
1·32 mm long in the 32 mm animal. Tsusaki (1922) described the division of the hyoid of
H. nebulosus into ceratohyale and hypohyale in the 19 mm stage, and ceratobranchiale and
hypobranchiale I and II are delimited at 11·5 mm. Ceratohyale and hypohyale are
extant in the 34 mm *H. leechii* but the hyoid is undivided at 17 mm (Matumoto 1932).
Further, *H. leechii* has ceratobranchiale and hypobranchiale I at 13 mm and cerato-

branchiale and hypobranchiale II at the 17 mm stage. The 30 mm *H. nebulosus* possesses ceratohyale and hypohyale, ceratobranchiale and hypobranchiale I, II and III and cerato-branchiale IV (Edgeworth 1923 *b*). Hypobranchiale III is present at 19 mm in *H. nebulosus* (Tsusaki 1922), and at 25·5 mm in *H. leechii* (Matumoto 1922); it was not figured in a 35 mm *H. keyserlingii* (Bogoljubsky 1925), but the hyoid and branchiale I and II were divided in this specimen. Hypobranchiale III is present in a 35 mm *Salamandra maculosa* (Stadtmüller 1936) and a 30 mm *Onychodactylus japonicus* (Okajima 1922). It is absent in *Cryptobranchus japonicus* (Fukuda 1928). The adult *Hynobius* possesses two branchial bars only, in addition to the complex hyoid (Wiedersheim 1877; Drüner 1904; Tsusaki 1922; Bogoljubsky 1925; Matumoto 1932; Stadtmüller 1936, p. 668; Hilton 1946). Similarly the adult of *Onychodactylus japonicus* (Okajima 1908), *Cryptobranchus japonicus* (Schmidt, Goddard & van der Hoeven 1864; Hyrtl 1865; Drüner 1904), *Salamandrella* and *Batrachuperus* (Hilton 1946), *Ranodon* (Wiedersheim 1877) and probably all caducibranchiate urodeles possess two branchiale. The adult *Menopoma* (*C. alleghaniensis*) exceptionally maintains a larval condition, and retains a hypobranchiale III (Fischer 1864; Parker 1882; Wiedersheim 1877), or even a hypobranchiale IV (Drüner 1904). The urobranchiale (post-copula) is continuous with the copula in *Hynobius*, differing from *Cryptobranchus* where it has either arisen independently (Fukuda 1928; Aoyama 1930), or, as thought by Edgeworth (1920), has developed as a ventro-posterior process from the 2nd basibranchial and subsequently separated.

The (paired) arytenoid cartilage (s. pars laryngeus cartilaginis lateralis) is procarti-laginous in the 14 mm stage, like the early condition of the hyobranchiale elements, but even at this early stage the dilator laryngeus is inserted upon it. It is a cylindrical carti-laginous rod 160 μ long at 17 mm and 290 μ long in the 22 mm form. A procartilaginous tracheal cartilage (s. pars trachealis cartilaginis lateralis) is first recognizable in the latter stage. At 32 mm the 500 μ long arytenoid lies alongside the larynx, and it is slightly flattened dorso-ventrally where the ligament of the dilator laryngeus inserts upon it (figure 48, plate 6). Just behind the sphincter laryngeus muscle is the blastema of the tracheal cartilage, and 170 μ further behind, in the dorso-mesial region of this blastema (alongside the trachea) the (cartilaginous) tracheal cartilage is recognized, about 530 μ long. The tracheal cartilage is situated 30 to 40 μ behind and separate from the arytenoid (figure 24). The tracheal and arytenoid cartilages are continuous in *Megalobatrachus*, *Amphiuma*, *Siredon*, *Proteus*, *Siren* and *Ellipsoglossa* (s. *Hynobius*), but separated in *Salamandra* and *Triton* (Edgeworth 1920, p. 130). The arrangement in the larval *Hynobius* of this work demonstrates that these cartilages arise independently of one another, although Edgeworth (1920, p. 156) considered the tracheal cartilage to arise as a non-chondrified backwardly directed growth of the arytenoid, which either chondrified or remained unchanged.

(3) *The ossifications*

Membrane bones

The toothed premaxilla is fused with its partner at the extreme front of the head. It has an ascending process in the 14 mm stage, which extends dorso-mesial to the nasal capsule in the 32 mm specimen. In the latter a posterior flange, separated from the premaxilla by about 20 μ, lies against the fenestra lateralis; it is the maxilla associated with teeth. The prevomer is situated mesial to the floor of the nasal sac and likewise bears teeth. The

palatine, which arises in continuity with the pterygoid, behind the prevomer and underneath the lamina orbito-nasalis, is associated with eight separate tooth germs on each side of the head in the 32 mm stage. Behind the teeth-bearing region the toothless pterygoid lies mesial or ventral to the processus pterygoideus to end against the inner surface of the quadrate cartilage. An almost vertical strut-like squamosal (Thyng, 1906) flanks the quadrate cartilage and the auditory capsule. The median sheet-like parasphenoid extends along the floor of the chondrocranium for further support. In the 32 mm form only, a nasale lies above the nasal capsule to fork over the premaxilla spindle in front, and behind, it lies over the frontal. The latter is a longitudinal strip of bone which extends from the nasal capsule to where it meets its fellow of the other side over the mid-brain. In the 32 mm stage the paired separate parietals completely cover the brain from about half way along the orbit to the tectum synoticum. The teeth-bearing dentary is fused with its fellow in the median anterior symphysis, and embraces the lateral surface of Meckel's cartilage. An anterior tooth-bearing coronoid (spleniale) is recognized against the mesial surface of Meckel's cartilage, and behind this there is a toothless goniale (prearticular), which covers the majority of the mesial surface. The goniale is not recognized in the 14 mm stage. A separate angulare lies beneath Meckel's cartilage and ends at the posterior limit in all specimens. This separate ossification is present in *Cryptobranchus japonicus* (Fox 1954), and also in *C. alleghaniensis, H. nebulosus, Salamandrella, Ranodon* and *Hypogeophis* (Stadtmüller 1937).

TABLE 1. LENGTHS OF THE OSSIFICATIONS (IN MM APPROXIMATELY) IN
VARIOUS STAGES OF *H. NEBULOSUS* LARVAE

	14 mm	17 mm	22 mm	32 mm
premaxilla	0·16	0·16	0·19	0·20
maxilla	—	—	—	0·30
prevomer	0·20	0·23	0·37	0·52
palatine	0·14	0·18	0·18	0·26
pterygoid	0·45	0·59	0·78	1·48
squamosal	0·44	0·64	0·64	1·64
parasphenoid	0·61	0·98	1·50	2·93
nasale	—	—	—	0·42
frontal	0·38	0·60	0·74	1·12
parietal	0·40	0·92	1·34	1·85
post-copula (oss)	—	—	—	0·08
dentary	0·90	1·01	1·54	1·69
coronoid (spleniale)	0·34	0·34	0·52	0·62
goniale (preart)	—	0·59	1·04	1·43
angulare	0·53	0·55	0·83	1·18
exoccipital	—	—	—	0·46

'artilage bone

In the 32 mm stage only, exoccipitals and some slight ossification in the post-copula and hypobranchiale II of the branchial skeleton are recognized. The exoccipitals extend from the posterior mesio-dorsal surface of the auditory capsule, back over the occipital arch. They are situated in front of, and segmentally arranged with, the more posterior neural ossifications, which brace the vertebrae and provide further skeletogenous support (figure 23). The vertebral centra are beginning to ossify. All the ossifications described are paired except where otherwise stated, and the lengths during development are shown in the accompanying table (table 1). Chung (1932) reported in *H. leechii* the origin of the

premaxilla and vomer at 12 mm; the nasale (15 mm); frontal (17 mm); maxilla (20 mm); prefrontal and palatine (34 mm); lachrymal (37 mm) and nariale (septomaxilla) just before metamorphosis: at 50 mm (Chung 1929). A septomaxilla was reported in the adult *H. leechii* by Lapage (1928). Yatabe (1931) who also described the origin of the septomaxilla just before metamorphosis, recognized the origin of the premaxilla, vomer and maxilla somewhat later than did Chung. It may be assumed from these results that the lachrymal, prefrontal and septomaxilla normally develop late, which explains their absence in the 32 mm *H. nebulosus*.

(4) *The musculature*

For convenience the musculature is arbitrarily divided into three groups. These are: (*a*) the muscles which deal specifically with jaw movement; (*b*) the post-hyoid upper pharyngeal musculature; (*c*) the ventral branchial muscles.

(*a*) *The jaw muscles* (figures 2, 7, 24)

The three separate muscles which raise the lower jaw, are collectively termed the masseter (figure 34, plate 5; figure 40, plate 6). The large innermost levator mandibulae anterior (M. adductor mandibulae internus (Luther 1914)) is inserted above on the crista trabecula, at the top of the processus ascendens, and is thence directed downwards to attach to the mesial surface of Meckel's cartilage. In the 32 mm specimen the upper portion leads behind along the upper surface of the brain to the tectum synoticum, where it joins its partner over the parietal bone (figure 24). There is a suggestion of division into an outer supratemporalis and an inner pterygoideus. The smallest levator mandibulae posterior (M. adductor mandibulae posterior (Luther 1914)), attached to the top of the quadrate cartilage, is situated lateral to the preceding muscle and leads ventro-anteriorly, to insert on the upper surface of Meckel's cartilage. The levator mandibulae externus (M. adductor mandibulae externus (Luther 1914)) arises at the top of the processus oticus, in the 14 and 17 mm stages, and on the squamosal in the older specimens (figure 42, plate 6). It is directed antero-ventrally outside the other levators, separated from the levator posterior by the r. mandibularis V, and is attached to the dorso-lateral margin of Meckel's cartilage, about half-way along its length.

Behind the masseter and closely associated with the hyoid is the massive depressor mandibulae or digastricus (M. cephalo-dorso-mandibularis (Drüner 1901; Litzelmann 1923)), which, when it contracts depresses the jaw. It is inserted on the posterior surface of the auditory capsule (figure 45, plate 6), below the levator arcus branchialis I, and is directed ventro-anteriorly lateral to the hyoid, above the ceratohyoideus externus and interhyoideus muscles, to attach on the ventro-lateral end of Meckel's cartilage. In the 32 mm stage there is a suggestion of a musculature attachment at the top of the hyoid on the left side. No attachment was recognizable in the 22 mm form but a definite one is clearly seen on both sides in the 17 and 14 mm specimens. The depressor mandibulae possesses a muscular insertion on top of the hyoid on both sides in the 27 and 37 mm *H. retardatus* specimens, and though no insertion was recognized in a 32 mm *Cryptobranchus japonicus* larva, definite insertions were apparent on both sides in 30 and 26 mm stages of this species and also in a 37 mm *C. alleghaniensis*.

(b) *The post-hyoid pharyngeal musculature* (figures 2, 7, 14, 24)

There are eight complexly arranged levatores arcuum branchialum muscles (figure 52, plate 7). In all specimens the first three levators are clearly recognizable. However as in *Cryptobranchus*, levators IV, V and VI are fused at their ventral regions (Fox 1954) (figures 38, 49, 53, plates 5 to 7), but the muscle mass is more compact and somewhat shortened in the antero-posterior plane in *Hynobius nebulosus*, and this feature, together with some distortion and muscle-fibre separation as a result of preparation, makes analysis difficult (figure 7 b).

Levator a. branchialis I arises on the posterior dorso-lateral surface of the auditory capsule above the digastricus. It leads postero-ventrally and ends on the upper mesial surface of branchiale I. It ends on the lateral surface of the latter in the 32 mm form.

Levator a. branchialis II arises behind levator I above the occipital somitic musculature. Levator II either has a common origin with the more posterior levator muscles as in the 14 and 22 mm stages, or has an independent origin in the 17 and 32 mm specimens. In every specimen examined, however, the muscle separates along its course and inserts on the mesial upper surface of branchiale II (figures 37, 53, plates 5 and 7).

Levator a. branchialis III has a clearly defined independent origin in the 32 mm form, but in the other specimens it is impossible to distinguish the upper limits of this muscle. It arises together with the more posterior levators as a common mass, but in all specimens a definite levator III separates off from this complex and clearly alone inserts on the upper mesial surface of branchiale III (figures 38, 49, 53, plates 5 to 7). Behind levator III are three more levators (levatores arcuum branchialum IV, V, and VI), in addition to the dilator laryngeus and trapezius muscles. Consideration of the figures 2 a, b, 7 a, 14 and the results in *H. retardatus* larvae strongly support this conclusion. The levators IV, V and VI are not as clearly apparent in the 32 mm stage (figure 24). The failure to observe the constituent muscular components clearly is probably the result of splitting of the original three muscles. The levators IV, V and VI which arise dorso-lateral to the head somites, attach at their common base to the upper mesial surface of branchiale IV. The dilator laryngeus (dorso-laryngeus or levator VII) is situated behind the preceding muscles and lateral to the trapezius (figures 50, 53, plate 7). It leads ventrally around the pharynx, and has a ligamentous insertion on the arytenoid cartilage (figure 48, plate 6). The trapezius (levator VIII) is a large sheet-like muscle situated mesio-posterior to the rest of the pharyngeal musculature (figures, 37, 38, plate 5).

(c) *The ventral branchial muscles* (figures 30–33)

The median transversely situated intermandibularis anterior (submentalis of Drüner 1901) is attached to Meckel's cartilage beneath the anterior symphysis. The cylindrically shaped geniohyoideus is attached in front to Meckel's cartilage above the intermandibularis anterior, and leads backwards above the intermandibularis posterior and inter-hyoideus muscles, to insert on the hind end of the post-copula. The ceratohyoideus externus inserted on the ventro-anterior margin of the hyoid in the 14 and 17 mm stages, or the hypohyale in later stages, leads posteriorly around the hyoid (figures 43, 45, plate 6) and is attached to the top of ceratobranchiale I. The ceratohyoideus internus (figure 43) arises at the antero-mesial surface of gill cleft I, just above the ceratohyoideus externus in

the 14 and 17 mm stages, and there is a further attachment at the junction of the cerato-
hyale and hypohyale in the 22 and 32 mm forms. The muscle is situated above the cerato-
hyoideus externus mesial to the hyoid, and it inserts behind on the lower surface of cerato-
branchiale I. The front of the constrictor arcuate musculature I–IV is situated just behind
the ceratohyoideus internus; there is an anterior attachment on the ventral surface of
ceratobranchiale I (constrictor arcuum I) (figure 45). The constrictor muscle leads
backwards lateral to the thoracicohyoideus, below the adductor arcuate muscles (figure 46),
and over the interhyoideus. There are further attachments on the ventral surfaces of
ceratobranchiale II and III (constrictors arcuum II and III), and it finally ends ventrally
on ceratobranchiale IV (constrictor IV).

The adductor arcuate muscles II and III (figures 45, 46) commonly insert on the copula,
and lead outwards below the thoracicohyoideus over the geniohyoideus, and then back-
wards, to attach to the lower surfaces of ceratobranchiale II and III. The large thoracico-
hyoideus, inserted in front between hypobranchiale I and the copula, above the branchial
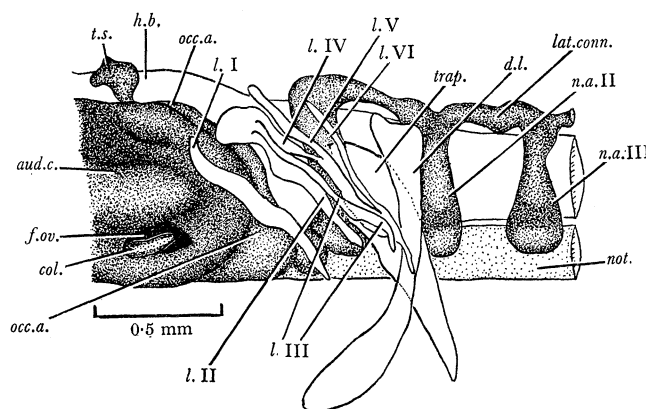

FIGURE 14. 22 mm stage *H. nebulosus*. Lateral reconstruction of the post-hyoid levator
muscles and anterior vertebrae of the left side.

plate, leads backwards surrounded by the hypobranchiale II above, ceratobranchiale II
laterally, and the copula below. It continues over the adductors and surrounds the heart,
arising behind from the pectoral girdle. Urodeles possess only a transversus ventralis IV
(Edgeworth 1935, p. 160), which in *Hynobius* joins its partner of the other side above the
heart and leads outwards to attach to the dorso-mesial surface of ceratobranchiale IV
(figure 48, plate 6). It is separated into two along its course. An omoarcualis leads from the
ceratobranchiale IV to the shoulder girdle. The ventral surface of the throat is covered
by intermandibularis anterior and posterior muscles; the latter is attached on either side to
the goniale. Behind, the interhyoideus situated between the geniohyoideus, intermandi-
bularis posterior and ultimately below the ceratohyoideus externus, is attached to the
paired hyoids (figures 43 to 45, plate 6). The gularis (constrictor colli) cannot be distinguished
from the interhyoideus, but muscle fibres which extend back into the opercular folds may
be the gularis constituent (Eaton 1936b), probably derived from posterior fibres of the
interhyoidei (Edgeworth 1923b). In the orbit of the 32 mm *Hynobius* a thin sheet-like
levator bulbi is attached in part above the lamina orbito-nasalis and the top of the pila
preoptica. Behind, it inserts on the anterior edge of the processes pterygoideus, like the

adult *Onychodactylus* (Matthews 1950), and underneath the eyeball. No division into the pars sagittalis, principalis or transversalis is recognizable. Below the eye it is closely associated with the r. maxillaris V, and in the orbit the r. ophthalmicus profundus V runs lateral and close to it. In all stages the external gill filaments (except filament IV) contain branchiarum muscles, innervated by the vagus nerves (figure 47, plate 6). A sphincter laryngis surrounds the laryngo-branchial skeleton in the 17 mm and older stages, and its front end lies just behind the 'dilator laryngeus-arytenoid' insertion (figure 48, plate 6). Its antero-posterior length is 70 μ at 17 mm, 0·1 and 0·23 mm long at 22 and 32 mm stages and proportionately thicker. Directed from the dilator laryngeus base the laryngeus
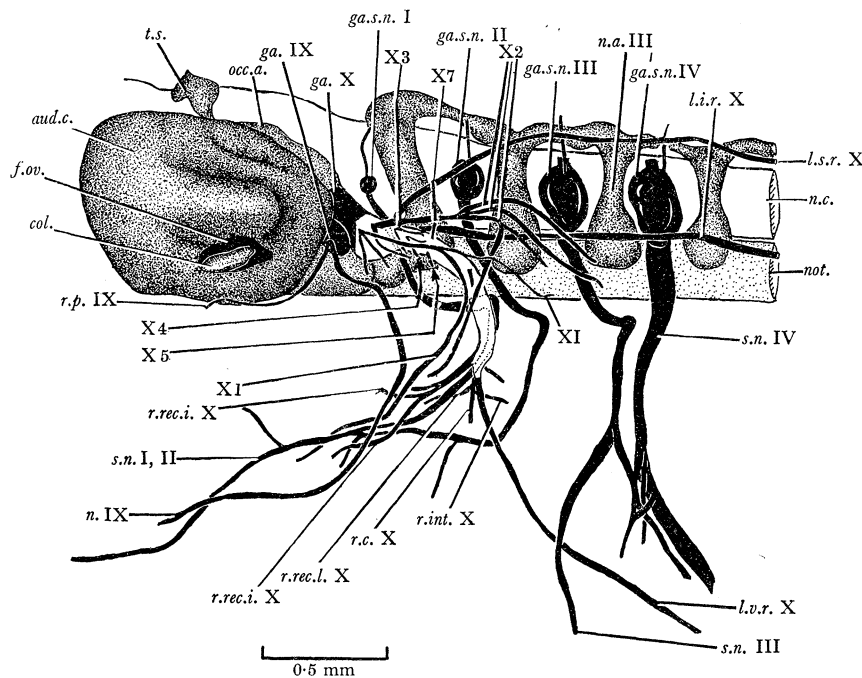

FIGURE 15. 22 mm stage *H. nebulosus*. Lateral reconstruction of the glossopharyngeal, vagus, truncus-intestino-accessorius and anterior spinal nerves.

ventralis continues antero-ventrally to an inscriptio below the larynx (see Goppert 1894; Wilder 1892, 1896), above but intimately associated with the transversus ventralis IV. No laryngeus dorsalis was recognized at any stage, in agreement with Edgeworth's results (1935, p. 172) in *Hynobius* and *Ambystoma*. The description of the jaw, post-hyoid and ventral branchial musculature is generally the same in *Cryptobranchus japonicus* larvae, as is the branchial musculature (Fox 1954), except for differences in size and rate of development. The arrangement of the ventral branchial muscles fully agrees with the description for *Hynobius* given by Edgeworth (1923 b), though the latter used a different nomenclature. The presence of levatores IV, V and VI in *Hynobius* larvae is a new feature hitherto not described except in *Cryptobranchus japonicus*.

(5) *The nervous system* (figures 5, 6, 10, 11, 28, 29)

The description will be specifically concerned with the arrangement in the 32 mm stage (figures 28, 29), but the pattern is generally the same in other specimens. For a consideration of the cranial nerves in larval urodeles the reader is referred to a previous work (Fox 1954).

The olfactory nerve I emerges from the olfactory lobe through the foramen olfactorius, beneath the r. nasalis internus V, by two roots together about 50 to 60 μ thick. A postero-dorsal division and upper and lower anterior ones, are distributed to the nasal sac.

The optic nerve II emerges through the optic foramen and leads ventro-anteriorly, beneath the profundus and over the r. ciliaris, to the eye.

The oculomotor nerve III arises at the ventro-lateral margin of the mid-brain, and runs forwards within the chondrocranium for 80, 120, 190 and 460 μ respectively in the 14 to 32 mm stages. It leaves the chondrocranium with the supraorbital artery through a
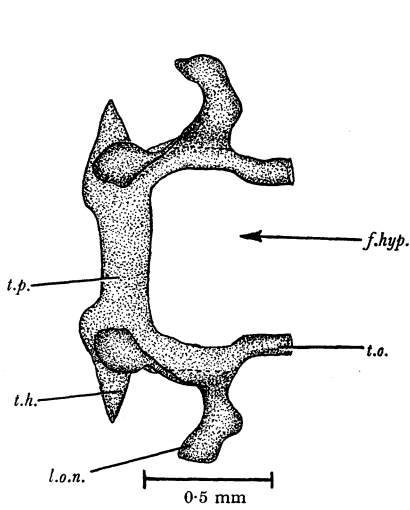

FIGURE 16. 17 mm stage *H. nebulosus*.
Dorsal reconstruction of the cartilage
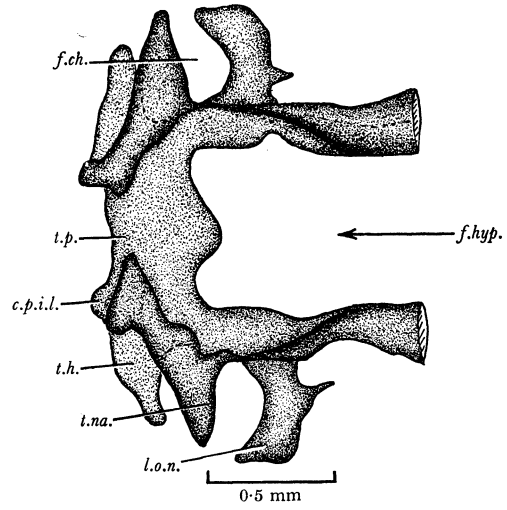of the nasal capsule region.

FIGURE 17. 22 mm. stage *H. nebulosus*.
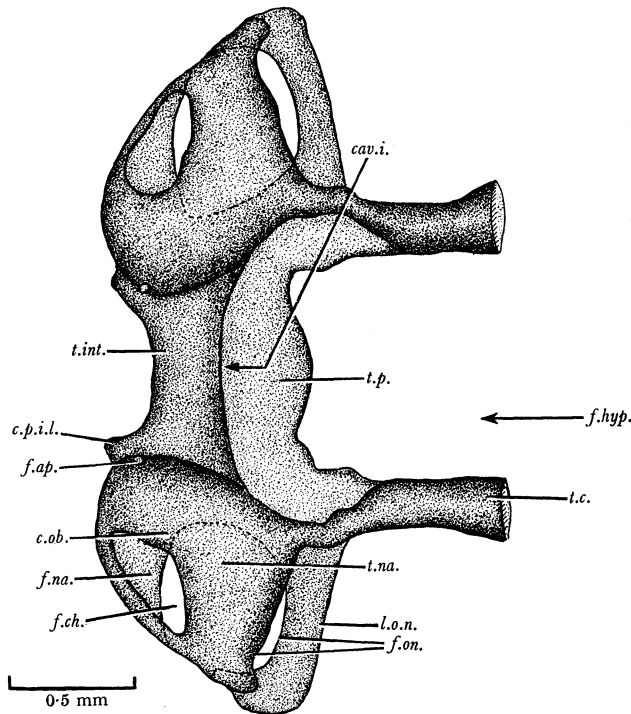Dorsal reconstruction of the cartilage
of the nasal capsule region.

FIGURE 18. 32 mm stage *H. nebulosus*. Dorsal reconstruction of
the cartilage of the nasal capsule region.

common foramen in the 14 and 17 mm stages, but emerges through a separate foramen oculomotorius in the 22 and 32 mm stages (figure 28). The nerve divides into two branches above and below the profundus, which nerves further divide to innervate the eye muscles, except the superior oblique and rectus posterior (r. externus). A large nerve ciliaris leads to the mesial surface of the eye. The latter is absent in the 14 mm form, nor was a ciliary ganglion recognized at any stage.

The delicate trochlear nerve IV, unrecognizable in the 14 mm stage but present in the others, is about 10 μ in diameter. It arises in the upper mid-brain, near the front of the auditory capsule, and runs forwards within the chondrocranium to emerge over the crista trabecula, mesial to the levator mandibulae anterior. It continues mesial to the two divisions of the first upper profundus branches and then lateral to the second upper profundus nerve, close to the top of the crista, and then dips down to innervate the superior oblique muscle. It is 1·22 mm long in the 32 mm stage.

The abducens nerve VI emerges from the chondrocranium through a small foramen abducentis at about the level of, but mesial to, the facial ganglion (figure 44, plate 6). Its origin, from the ventral surface of the hind-brain, is, however, further back, at about the level of the fenestra perilymphatica (figure 46, plate 6). In the 22 mm stage the distance traversed through the foramen abducentis is 140 μ. Nerve VI continues forwards close to the trabecula, over the parasphenoid, mesial to the r. palatinus VII, and curves upwards internal to and then over the rectus posterius which it innervates (figure 40, plate 6). It is about 1 mm long and slightly thicker than the trochlear nerve.

The trigeminus nerve V

(a) The ramus ophthalmicus profundus V is generally similar in all stages but more complicated in arrangement in the 32 mm stage (figure 28). The profundus nerve, which is an anterior continuation of the trigeminus ganglion (the latter showing no sign of its dual origin) leads inside the processus ascendens (figures 40, 41, plate 6) and between the upper and lower divisions of the oculomotor nerve. It gives off two upper divisions, both of which divide and innervate the upper skin. There is close association, but no anastomosis, between them and the r. superior ophthalmicus facialis. Before reaching the nasal capsule the profundus divides into three.

(i) The upper branch (r. nasalis internus profundus V) divides again before entering the orbito-nasal foramen. The main nerve runs mesial to the nasal sac over the olfactory nerve, together with another subdivision which ends over the latter, and thence lies below the supraorbital artery, and with the latter leaves the capsule through the foramen apicale, to innervate the skin at the tip of the snout. A small external division, which does not enter the capsule, leads to the skin at the anterior margin of the eye.

(ii) The middle profundus division (r. nasalis externus profundus V) gives off two delicate branches to the skin of the lateral snout and then forthwith enters the nasal capsule lateral to the nasal sac. A delicate branch leaves the capsule via the foramen lateralis, to join the main nerves which emerge through the foramen narina, to innervate the skin of the anterior snout.

(iii) The ventral profundus division gives off a palatine-profundus branch to the palatine nerve, and a deep profundus (only suspected in the 14 mm stage) which joins the

inner portion (mainly r. buccalis VII fibres) of the truncus-infraorbitalis. From the 'truncus-infraorbitalis-profundus' complex, a nerve leads forwards behind the internal naris, over the r. palatinus VII and thence mesial to the nasal sac. It lies below the other profundus nerves along its course, and finally leaves the capsule by its own tiny foramen in the anterior surface, to innervate the skin. In different specimens of *Hynobius* larvae the arrangement of the anterior nasal profundus branches no doubt shows variability within the general pattern described.

(*b*) The r. maxillaris V separates from the r. mandibularis V at the inner forward end of the auditory capsule (figure 40, plate 6) and emerges over the processus ascendens. It is practically separate from the r. buccalis facialis at 17 mm (figure 10) but fused anteriorly in the 14 mm specimen (figure 5). There is some mixing of fibres at 22 mm, and the two nerves join (truncus infraorbitalis) in the 32 mm stage (figure 28) lateral to the levator mandibulae anterior. The r. maxillaris V is situated ventro-mesial to the r. buccalis facialis (the latter probably containing some maxillary fibres) when it becomes free below the eye, and it is distributed to the skin of the upper jaw.

(*c*) The r. mandibularis V emerges over the processus ascendens (figure 34, plate 5) and thence sends off branches to the masseter. The main branch leads between the levator mandibulae externus and posterior muscles, lateral to the dentary and divides into the following:

(i) A r. mentalis V which runs forwards between the levator mandibulae externus and the dentary, but never enters the latter, to innervate the skin of the lower jaw; (ii) a r. intermandibularis V runs almost vertically between the dentary and Meckel's cartilage to divide on emergence and then innervate the intermandibularis muscles; (iii) a division arises just behind the r. intermandibularis which leads vertically alongside the jaw. After sending off an anterior branch which joins the r. mentalis externus facialis about 460 μ further forwards (not seen in the 14 mm form), then it forks close to the skin. The upper r. mentalis V is completely separate from the r. mentalis externus facialis in all stages. The 14 mm specimen possesses a well developed balancer; its skeletogenous tubular sheath inserted at its base on the quadrate cartilage terminates about 60 to 70 μ from the end. Inside the balancer is the balancer nerve, a division of the r. mandibularis V (figure 35, plate 5). A nerve to the balancer has been reported in the early swimming stage of *Ambystoma* (Penfold & Roofe 1956), and together with blood vessels in *H. fuscus* (Murayama 1928). With the loss of a balancer in the 17 mm and later stages of *Hynobius*, these specimens possess a vestigial balancer nerve, leading posteriorly mesial to the levator mandibulae externus, towards the vestigial skeletogenous base on the quadrate cartilage.

The facialis VII nerve

The r. superior ophthalmicus facialis leads forwards close to the skin, over the levator mandibulae anterior and the eye, embraced along its course by the dorsal branches of the profundus, to end at the tip of the snout over the nasal capsule. The lower r. buccalis facialis is associated with the r. maxillaris V and profundus as previously described for the truncus-infraorbitalis. The predominantly buccalis fibres, when they separate, lie slightly latero-dorsal to the maxillary nerve and innervate the lateral line organs at the side of the upper jaw. The r. palatinus facialis is separated from the r. hyomandibularis

facialis by a chondrified post-palatine commissure in the 22 and 32 mm stages (figures 13, 27; figure 43, plate 6), though there is an incipient fibrous commissure in the 17 mm form; hence these nerves emerge by separate foramina from about this stage onwards. The palatine nerve leads forwards over the pharynx and below the basitrabecular connexion (figure 42, plate 6), lateral to the abducens nerve, beneath the rectus posterior and trabecula, inside the nasal capsule close to the inner margin of the foramen choanalis, to innervate the prevomerine teeth. It receives a palatine-profundus nerve mesial to the posterior nasal sac region. In the 32 mm stage an incipient lateral division runs for a short distance lateral to the internal naris. No palatine-caudalis was recognized in any specimen.
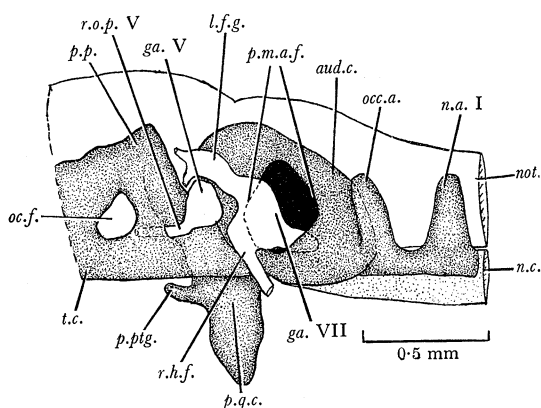

FIGURE 19. 14 mm stage *H. nebulosus*. Lateral reconstruction of the mesial surface of the auditory capsule and related ganglia.
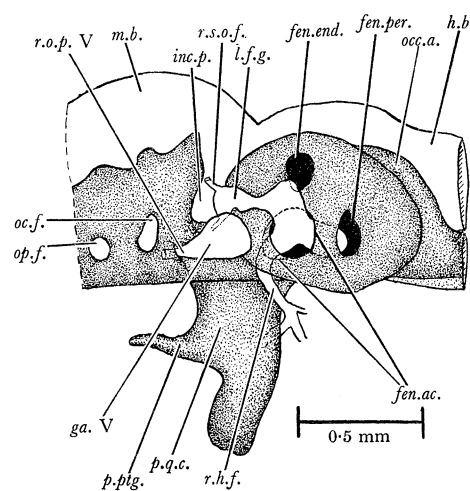
FIGURE 20. 17 mm stage *H. nebulosus*. Lateral reconstruction of the mesial surface of the auditory capsule and related ganglia.

The origin of the r. hyomandibularis facialis is between the mesial prefacial commissure and the lateral auditory capsule, at about the level of the fenestra acoustica anterior (figure 44, plate 6). On emergence from the chondrocranium it divides into three main branches:

(i) A r. mandibularis externus facialis leads ventro-anteriorly around the back of the quadrate cartilage, between the masseter and digastric muscles, and subsequently divides into two. The upper r. mentalis externus facialis receives a small branch from the r. mandibularis V and then innervates the lateral line system of the skin of the lower jaw. A lower r. mentalis internus facialis runs around the back of Meckel's cartilage below the jaw and divides into two to innervate the neuromast system of the skin below the intermandibularis muscle. Along its course it lies mesial to the hyoid cleft, but lateral to the hyoid, and anastomoses with a branch of the r. intermandibularis V.

(ii) A r. mandibularis internus facialis (r. alveolaris VII) separates from the r. hyomandibularis facialis, mesial to the r. mandibularis externus VII, and leads almost vertically downwards just behind the quadrate cartilage. It runs forwards below the latter, between Meckel's cartilage (lateral to it) and the hyoid cleft, and then continues on between Meckel's cartilage and the goniale, giving off a small upper branch traversing a small foramen in the goniale and leading inwards towards the hyoid cleft. The main

nerve proceeds forwards, between the rim of the goniale and the coronoid, and supplies the teeth of the latter.

(iii) The outermost r. jugularis facialis joins the other divisions of the hyomandibular nerve just behind the quadrate cartilage. Its course is postero-ventrally through the
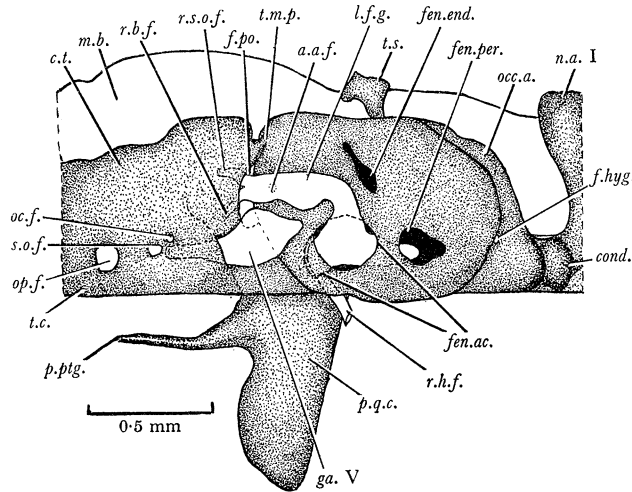

FIGURE 21. 22 mm stage *H. nebulosus*. Lateral reconstruction of the mesial surface of the auditory capsule and related ganglia.
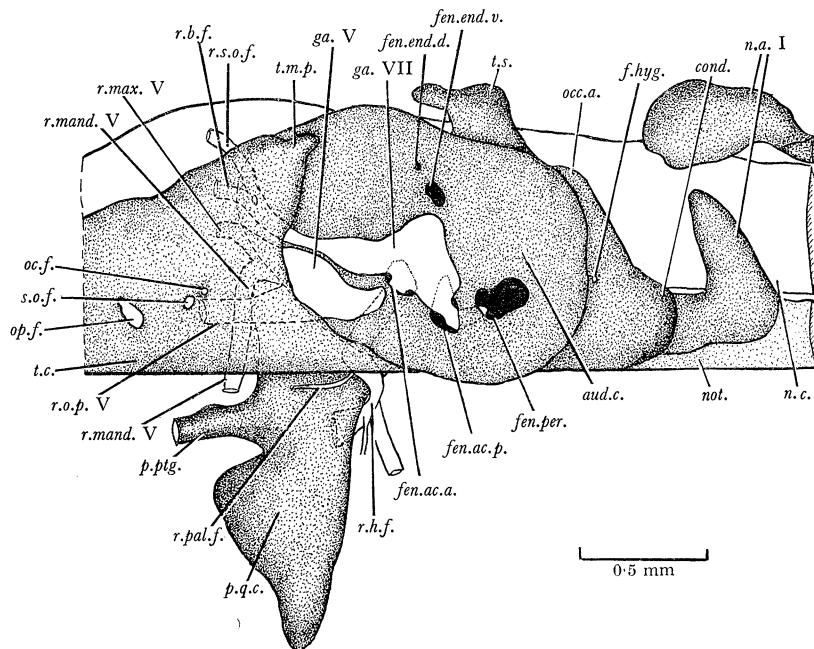
FIGURE 22. 32 mm stage *H. nebulosus*. Lateral reconstruction of the mesial surface of the auditory capsule and related ganglia.

digastric which it innervates. In the 32 mm stage there are five secondary divisions; upper branch I leads postero-laterally to the hind surface of the digastricus and it innervates the ceratohyoideus externus. In descending order branch II leads back on the surface of the latter muscle which it likewise innervates; branch III leads back on the surface of the ceratohyoideus externus and ultimately innervates the interhyoideus; branch IV similarly

leads to the interhyoideus; branch V runs forwards, below the interhyoideus and cerato-hyoideus externus, lateral to the r. mentalis internus facialis. It ramifies with the latter and distribution is to the interhyoideus and the skin. The VII–IX Connective of Willis continues backwards from the hyomandibular nerve against the columella stilus and below the columella, lateral to the head vein, mesial to the top of the digastricus to which it distributes several fine branches, over the r. pharyngeus IX and finally it joins the glosso-pharyngeal nerve IX at its origin (figures 28, 29). In the 14 and 17 mm specimens a small unbranched nerve arises above the junction of the rami superior ophthalmicus and buc-calis, and it leads behind around the auditory capsule (figures 5, 10). There are two small nerves in the 22 mm form, and two complexly branched nerves arise from the upper surface of the r. buccalis only in the 32 mm stage (figure 28). These nerves are probably the r. oticus which are distributed to the lateral line organs of the auditory region. In all stages two nerves possessing a common origin arise from the upper surface of ganglion X, above nerve IX. The anteriorly directed r. auricularis innervates the skin of the posterior auditory region, and the posterior r. supratemporalis leads through the levator muscles to the neuromasts of the occipital region. The paired nerves are designated the r. supra-temporalis et auricularis. No connexion between the latter and the r. oticus was recognized. The glossopharyngeal nerve IX, which arises from its own ganglion, is composed of a r. pharyngeus IX which separates from the r. post-trematicus IX behind the auditory capsule. It leads forwards below the VII–IX Connective of Willis and ultimately below the lateral aorta, and innervates the pharynx roof. The r. post-trematicus IX leads backwards to innervate the levator I and then it curves forwards mesial to the cerato-hyoideus externus which it innervates. It leads on lateral to branchiale I and a lower division innervates the ceratohyoideus internus. The upper division again branches, one branch ending alongside the anterior copula underneath the floor of the mouth, and the other continues above the junction of the hyoid and copula, and terminates above the extreme anterior end of the latter.

The vagus nerves X (figures 5, 10, 29)

The vagus branchial nerve I consists of a pre-trematic, post-trematic and pharyngeal ramus in all specimens. Vagus post-trematicus I at 32 mm runs posteriorly for about 0·5 mm below levator II and innervates it. After giving off a posteriorly directed branch to the muscles of external gill filament I it curves forwards, behind gill slit II and situated below branchiale II. A small division leads between the constrictor and adductor arcuate muscles, which ends in the anterior portion of the constrictor. The main branch continues forwards above the adductors, below branchiale II and lateral to the thoracicohyoideus, to end on the floor of the mouth above branchiale II. The vagus pretrematicus I leads ventro-anteriorly and ends above the roof of the lateral pharynx. The tiny vagus r. pharyn-geus I is directed ventrally to the pharynx roof. Vagus branchial nerve II has pre- and post-trematic rami in all specimens. A pharyngeal ramus was not found on either side at 14 mm nor on the left in the 17 and 22 mm forms. It is present on the right in the latter and on both sides in the 32 mm specimen. The vagus post-trematicus II innervates the levator III, and then it divides into three. Branch I leads behind to the muscles of gill filament 2; branch II curves forwards behind branchiale III, and has a small posterior

division to gill filament 3 in the 17 and 22 mm forms (absent at 14 mm), which is well developed in the 32 mm stage. Branch III leads backwards in the upper region of gill filament 3. In the 32 mm form the delicate vagus pretrematicus II (140 μ long) leads postero-laterally to end over the lateral aorta and a fine pharyngeus II leads to the pharynx over the head vein. Vagus branchial nerve III is merely a post-trematic division on the left at 14 mm and on both sides in the 17 mm form. There are pre- and post-trematic rami on the right at 14 mm, on both sides at 22 mm and on the left side in the 32 mm specimens. On the right of the latter vagus III possesses pre-trematic, post-trematic and pharyngeal rami. In all cases on both sides of the head, except for the left in the 32 mm specimen when it could not be followed to its destination, post-trematic III ends in levator IV.

Vagus branchial nerves IV and V were not found in the 14 mm stage but extremely fine post-trematic rami IV and V were present on both sides in the 17 mm form. At 22 mm vagus IV consisted of a pre- and post-trematicus on the left and a post-trematicus only on the right; vagus V is a post-trematicus only on the left side but was not recognized on the other side. In the 32 mm form vagus IV consisted of pre- and post-trematic rami on the left side; its presence is doubtful on the other. Vagus V was not recognized on either side. In the 22 mm form vagus IV innervated levator V. The course of vagus V in these specimens could not be followed, but as in *Cryptobranchus* it no doubt innervates levator VI. Vagus branchial VI (figure 39, plate 6; figure 50, plate 7), recognizable in all specimens except in the 32 mm stage, leads outwards underneath the trapezius to innervate the dilator laryngeus. The stout vagus branchial VII, present on both sides of the head in all specimens, arises from the upper surface of the vagus ganglion and is distributed to the trapezius (figure 38, plate 5).

The truncus-intestino-accessorius X (figures 6, 11, 15, 29) lies lateral to spinal nerve I, and at the level between neural arches I and II it curves forwards and separates into anterior and posterior divisions. Where the truncus and spinal nerve I lead forwards there is intimate association between them. In the 32 mm stage a medial anterior r. recurrens intestinalis X (which may contain some spinal nerve I fibres), divides into two, the upper one again dividing into four to innervate the transversus ventralis IV. The lower division separates into two branches and innervates the constrictor muscles. A large r. lateralis ventralis X leads backwards from the truncus, lateral to spinal nerve II and the thoracico-hyoideus and inside the pectoral girdle, to innervate the lateral line organs of the body. The posterior truncus branches consist of (i) an upper r. gastricus X to the gut; (ii) a stouter lower r. intestinalis X dividing into several gastro-tracheal branches which lead to the region between the gut and trachea; (iii) a r. cardiac X to the heart; (iv) a pair of ventral r. recurrens laryngei X, both of which lead forwards one above the other to the larynx. Two upper lateralis nerves arise from the mesial surface of the vagus at about the level of spinal nerve I and lead posteriorly to the neuromasts of the body. Spinal nerves I and II do not join in the 14 and 17 mm stages but do so in the 22 and 32 mm forms (r. hypobranchialis). In the 32 mm stage spinal nerve I, which may have exchanged fibres with the truncus, joins spinal nerve II lateral to the thoracicohyoideus at the level of the occipital crest. This r. hypobranchialis innervates the thoracicohyoideus and the geniohyoideus muscles and terminates below Meckel's cartilage and the intermandi-

bularis anterior. It may innervate the latter, but actual termination of fibres was not recognized. Spinal nerves III, IV and V form the pectoral complex which innervates the posterior thoracicohyoideus and the complex musculature of the pectoral girdle and forelimb.
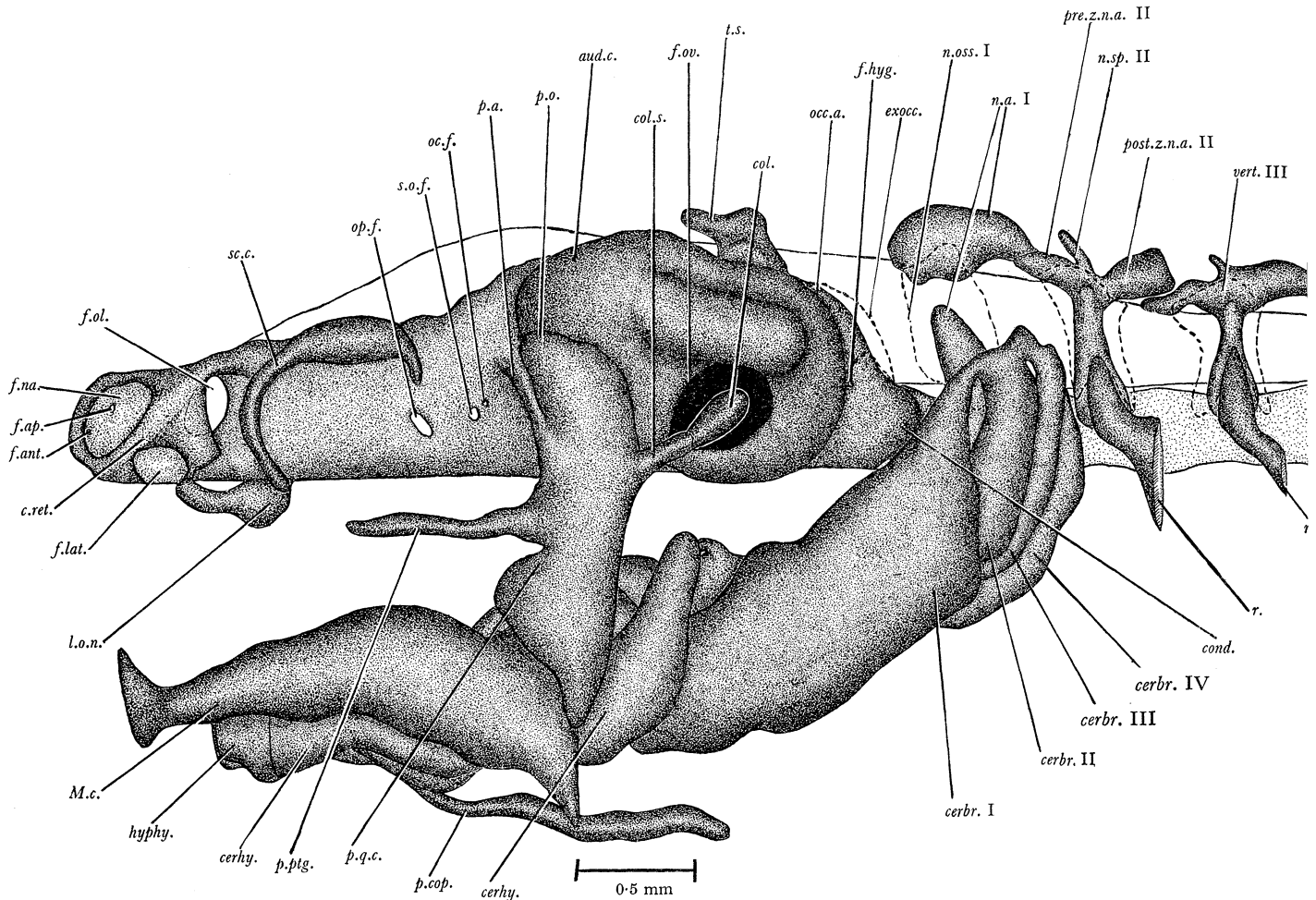

FIGURE 23. 32 mm stage *H. nebulosus*. Lateral reconstruction of the chondrocranium, jaw and hyobranchial skeleton and anterior vertebrae and ribs.

In *Hynobius* from 14 mm onwards there is a hyoid cleft and four open gill slits. A vestigial 5th gill cleft is present on the left side only at 14 mm and both sides in the 17, 22 and 32 mm specimens. A vestigial 6th cleft is recognizable on the left side at 22 mm and on both sides of the 32 mm stage (figures 36, 47, 49, plates 5 and 6). Furthermore a vestigial pair of 7th gill clefts is considered to be present in the latter; each is about 200 μ long and 50 μ behind and mesial to it is the front of the arytenoid (figure 55, plate 7). This topographic relationship is similar to that of the functional gill clefts and their related branchial bars. The laryngeal groove is about 70 μ behind the origin of the 7th cleft. All specimens possess a hyoid operculum (modified external gill filament) and four further external filaments, each one situated behind the four open gill clefts (figure 49, plate 6). On the left side of the 14 and 17 mm specimens a small protuberance, situated behind gill filament 4 and the vestigial gill cleft 5, is probably a vestigial 5th external gill filament. The structure is less clearly defined in the 22 and 32 mm forms.

THE BLOOD VESSELS OF THE HEAD

(6) *The arteries* (figures 9, 25)

Four afferent epibranchial arteries lead from the heart to the four external gill filaments and associate with four efferent arteries from the lateral aorta. The 4th efferent artery (aortic arch VI) gives off a prospective pulmonary artery to the lung. Leading from the upper surface of efferent 2 is the external carotid, which in the 32 mm stage divides into
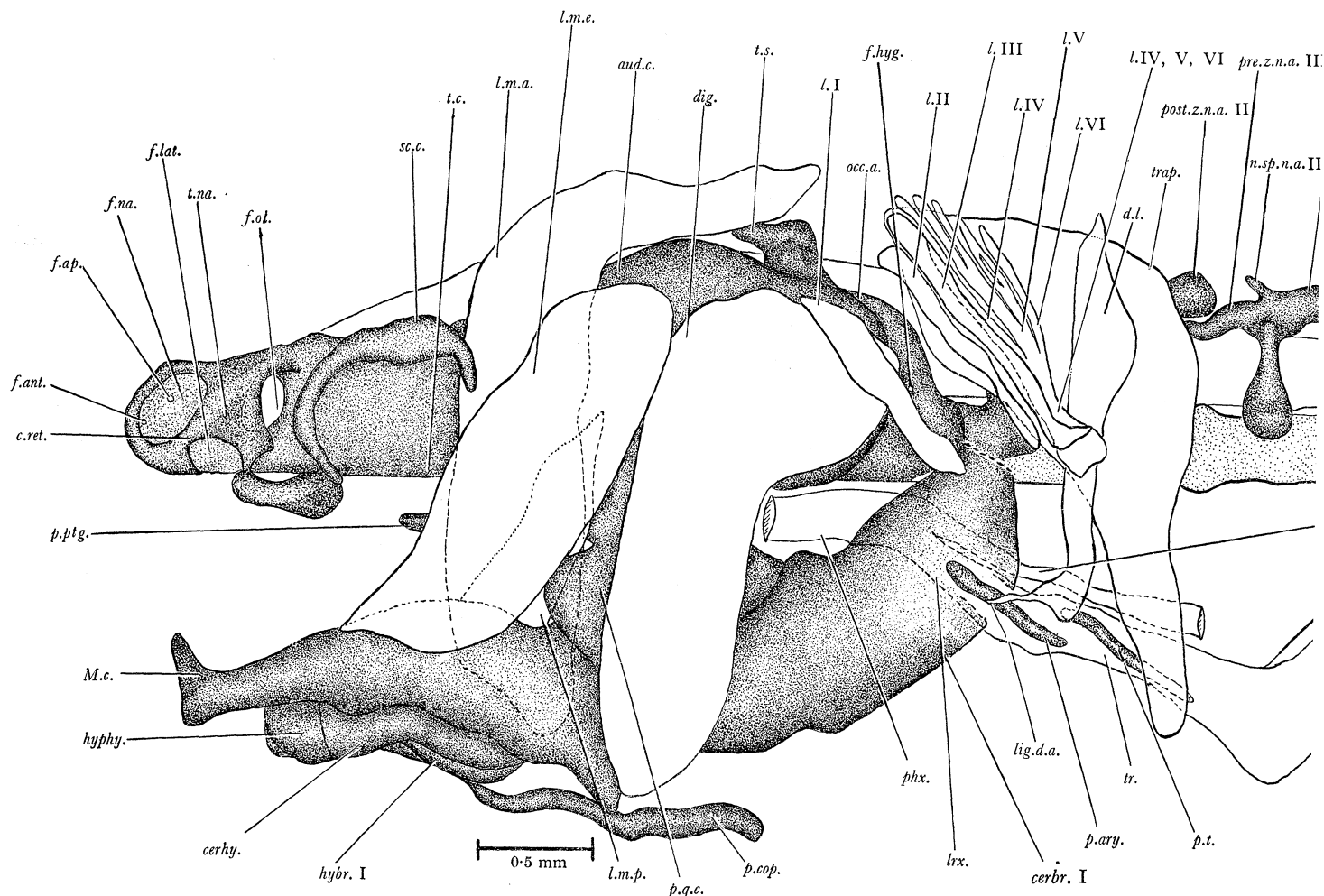

FIGURE 24. 32 mm stage *H. nebulosus*. Lateral reconstruction of the chondrocranium, jaw and part of the hyobranchial skeleton, laryngo-tracheal cartilages, jaw and post-hyoid levator musculature.

upper and lower vessels supplying the lateral surface of the digastricus. In front a hyoid artery leads from the lateral aorta mesial to the quadrate cartilage and lateral to the hyoid, and a palatine artery curves around the edge of the parasphenoid, to run forwards mesial to the palatine nerve over the roof of the mouth. Behind the hyoid artery in the 32 mm stage (first formed at 17 mm), the orbital artery (stapedial of mammals (de Beer 1926, p. 341)) leads forwards mesial to the columella stilus, lateral to the head vein and the front of the columella, between the otic and basitrabecular processes. It continues over the ascending process to the region between the levator mandibulae externus and mandibulae anterior muscles. The internal carotid enters the chondrocranium at the hind end of the

hypophysial fenestra and from it a supraorbital artery emerges from the skull again, through the supraorbital foramen. An upper branch of the latter enters the nasal capsule, mesial to the nasal sac, and leaves it together with the r. nasalis internus profundus V through the foramen apicale; a lower division supplies the inner surface of the eye. The rest of the internal carotid divides into a posterior carotis cerebralis, which joins its

FIGURE 25. 32 mm stage *H. nebulosus*. Lateral reconstruction of the chondrocranium and arterial blood system. Part of the hyobranchial skeleton is omitted.

opposite number behind, below the mid-brain, as the basilar artery and an anterior carotis cerebralis, which leads forwards along the side of the mid-brain. In the 32 mm form behind the auditory capsule there is a vertical occipital artery against the occipital crest, and a branch from efferent epibranchial III divides to supply the pharynx and the region between the trapezius and somitic musculature.

(7) *The veins* (figures 4, 9, 26)

In the 32 mm stage the vena capitis lateralis (main head vein) receives two vertebral veins which lie between the trapezius and somitic musculature, at the level of neural arch I. In front a cutaneous vein leads outwards, over vagus I and the levator muscles to the

skin. The large post-cerebral vein drains blood from the mid- and hind-brain. It arises, in common with its opposite partner below the tectum synoticum and leads backwards over the r. supratemporalis et auricularis X, mesial to the auditory capsule, vagus ganglion, and trapezius and meets the head vein lateral to the occipital arch. The main head vein is situated lateral to the columella, over the junction of the columella stilus and quadrate cartilage, then above the r. hyomandibularis facialis and mesial to the processus oticus. Half-way along the head vein separates into two. The upper division receives blood

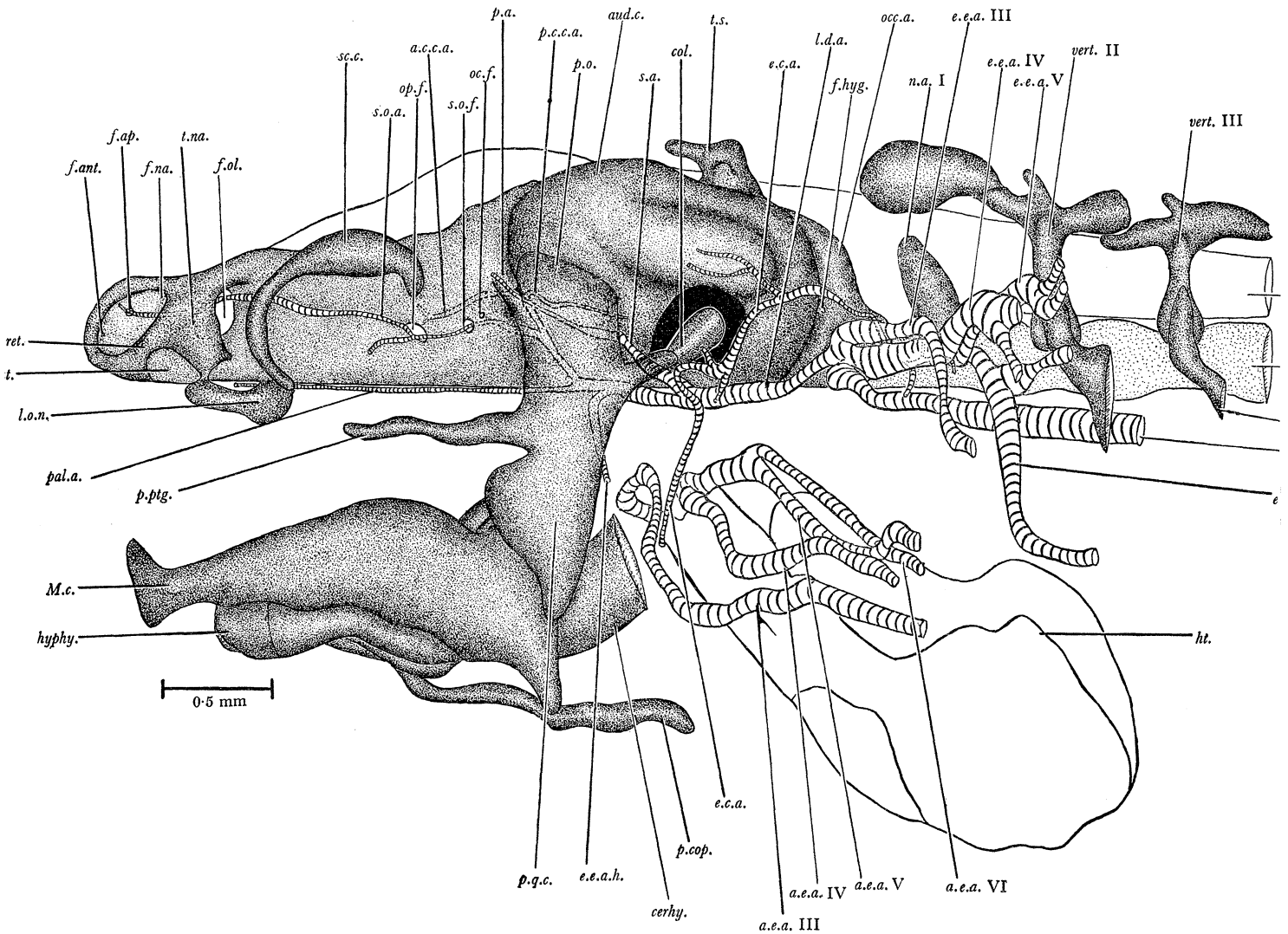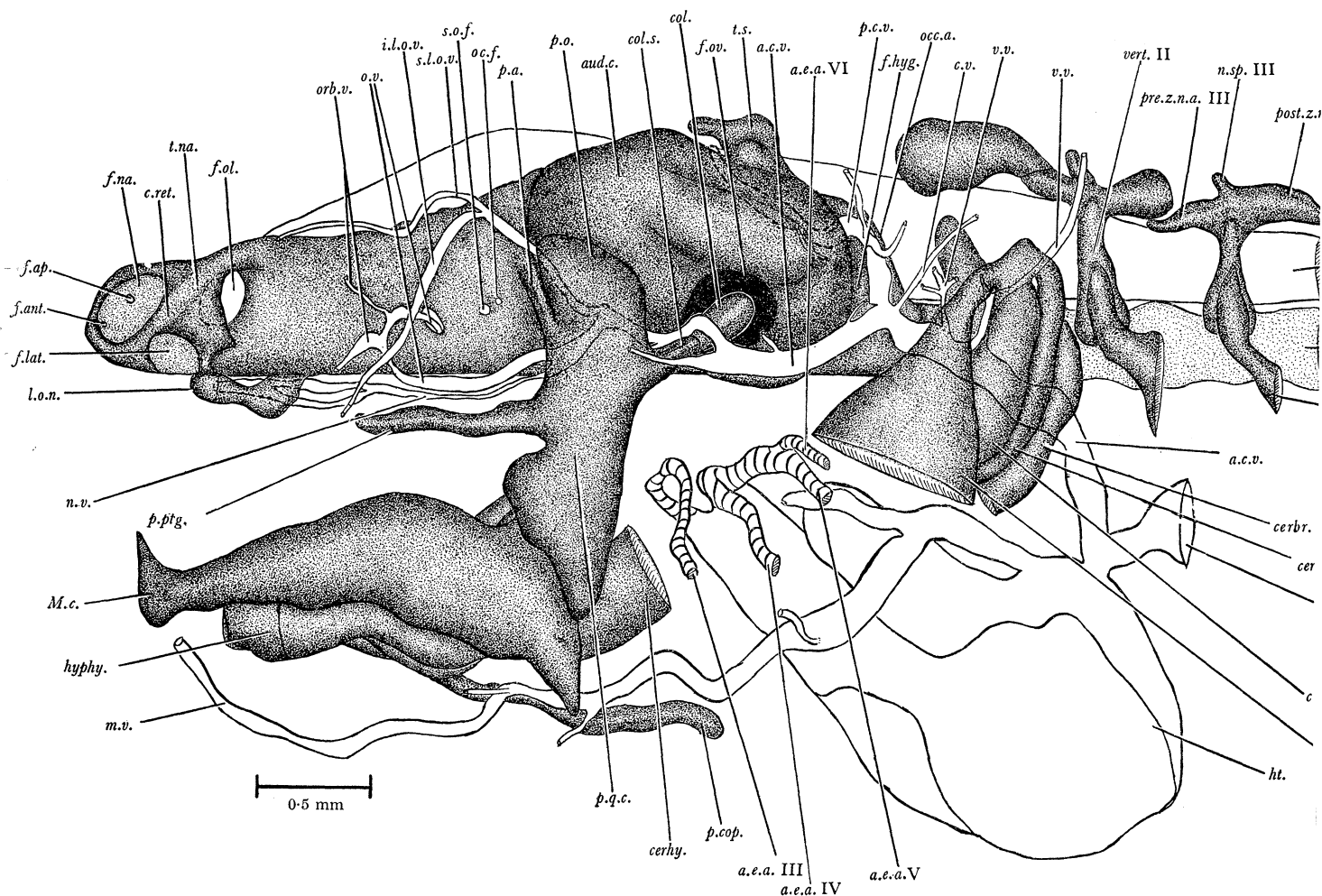

FIGURE 26. 32 mm stage *H. nebulosus*. Lateral reconstruction of the chondrocranium and venous blood system. Part of the hyobranchial skeleton is omitted.

from above and below the lateral surface of the eye (the two vessels meeting below the r. buccalis facialis); the lower division receives blood from the region lateral to the palatine nerve (nasal vein), the mesial surface of the eye (orbital veins), and a vessel emerging from the brain through the optic foramen (optic vein). A large mandibular vein of the lower jaw leads between the thoracicohyoideus and the geniohyoideus lateral to the copula. It meets the vein of the other side below the anterior end of the geniohyoids. A large post-cardinal sinus bathes the pronephros behind the heart. The venous pattern is similar but simpler in the other stages, although there is some variability in the arrangement of the anterior veins which may or may not lead to connexions between them (figures 4, 9).

Two specimens: 27 and 37 mm long: nose-to-cloacal lengths 12·81 and 15·48 mm respectively.

In both specimens balancers are absent but the vestigial base of the balancer membrane is recognizable. The forelimb is undivided on the left side in the 27 mm stage, but well formed with 4 digits on the right, and on both sides in the 37 mm specimen. The right forelimb is 3·21 mm long at 27 mm and 2·83 mm long (probably abnormally stunted) in
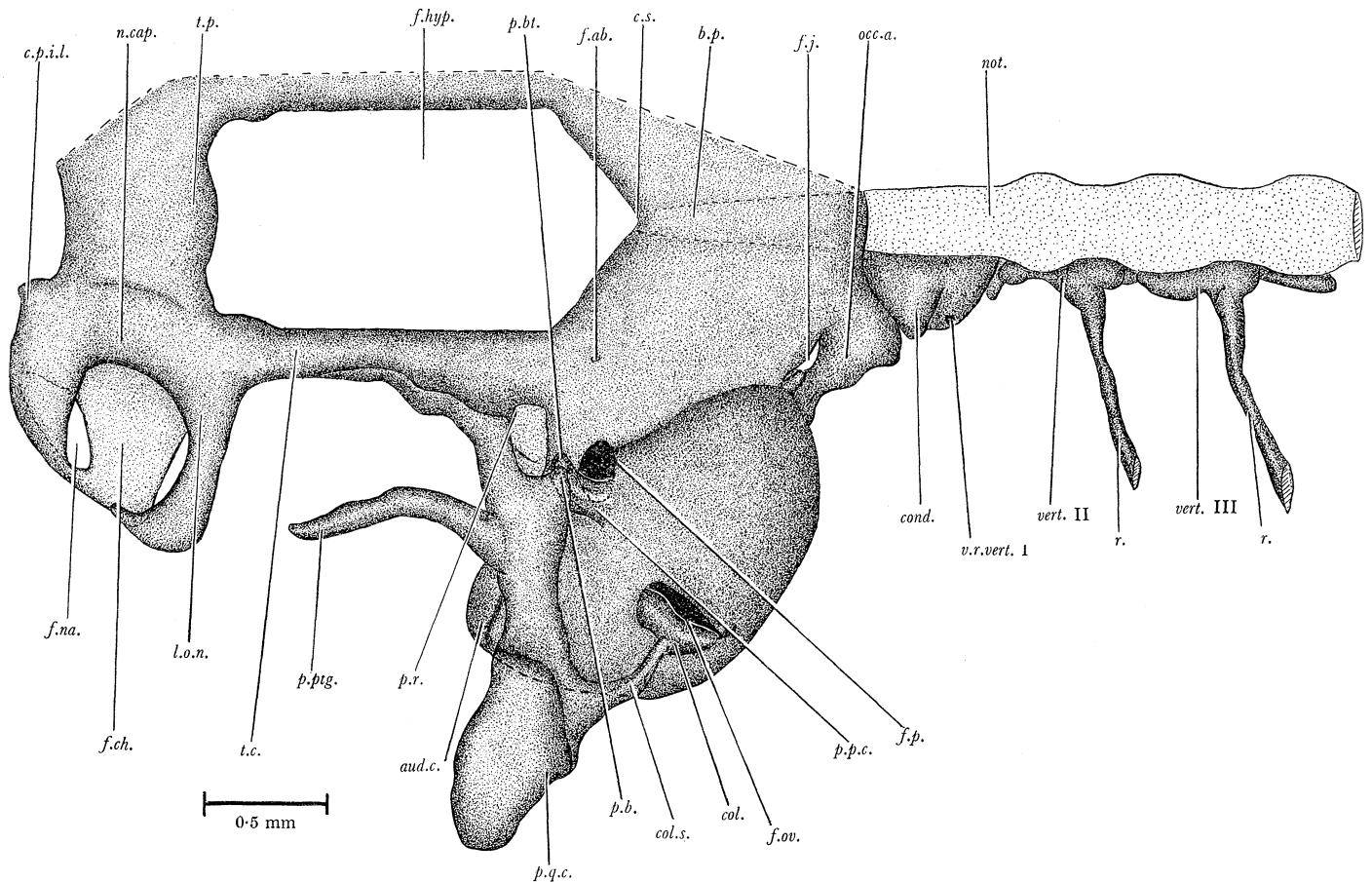
FIGURE 27. 32 mm stage *H. nebulosus*. Ventral reconstruction of part of the chondrocranium and anterior vertebrae.

the 37 mm stage. The left forelimb of the latter is 4·30 mm in length. The 27 mm stage possessed a flattened undifferentiated hindlimb on the right with no digital divisions visible externally. On the left in the latter and on both sides of the 37 mm form the hindlimbs are well developed and possess 5 digits.

The chondrocranium, jaws and hyobranchial skeleton of the 27 mm form of *H. retardatus* show features in general intermediate between those of the 22 and 32 mm *H. nebulosus* specimens. There are some differences however. The nasal capsule is similar to that in the 22 mm *H. nebulosus*, though the overall length of the chondrocranium of the latter, from the anterior end to the hind surface of the occipital arch is 2·80 mm, and the length to the back of the auditory capsule in the 27 mm *H. retardatus* is 3·50 mm. In the latter,

and also the 37 mm *H. retardatus* the large auditory capsule completely covers the prootic foramen and the occipital arch when viewed laterally. The nasal capsule of the 37 mm *H. retardatus*, though similar, is larger than in the 32 mm *H. nebulosus* but the posterior region of the planum tectale is less well developed, a fenestra lateralis has yet to form, and the anterior extension of the lamina orbito-nasalis is shorter. Further, there are separate oculomotor and supraorbital foramina in the 22 mm *H. nebulosus*, but no 'division' is
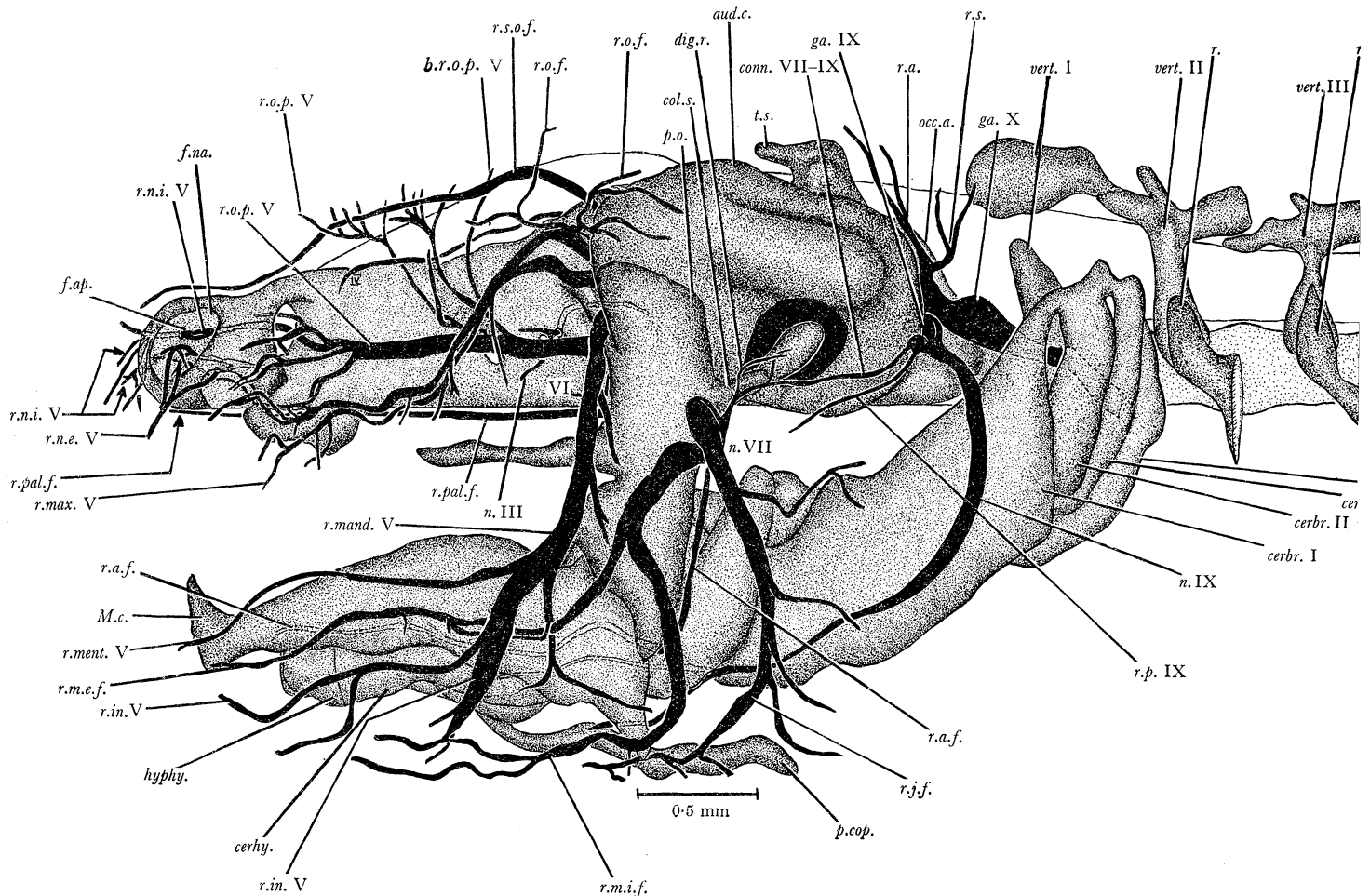
FIGURE 28. 32 mm stage *H. nebulosus*. Lateral reconstruction of the cartilage
and part of the cranial nervous system of the head and pharynx.

recognizable in the 27 mm *H. retardatus*. Separation has occurred on the right side of the 37 mm *H. retardatus*. The sclerotic cartilage of the 27 mm *H. retardatus* is a complete chondrified ring except for a gap of about 80 μ; it is complete in the 37 mm specimen. The processus pterygoideus is not chondrified throughout its length in the *retardatus* specimens in agreement with the results in the *nebulosus* group. A syndesmotic joint in the basal process is recognized in the 37 mm *H. retardatus*. There is no cartilaginous continuity between the columella and the pterygo-quadrate cartilage. A stream of cells, procartilaginous in appearance in the 37 mm specimen, leads from the columella to the lateral surface of the quadrate cartilage to merge into the region between the latter and the squamosal. The cellular connexion is about 280 μ long at 27 mm and 220 to 240 μ in the

37 mm stage. The tectum synoticum shows no sign of its paired origin. The foramina of the medial wall of the auditory capsule are similar to those in the 22 and 32 mm *H. nebulosus* stages, but the fenestrae acoustica anterior and posterior are merely separated by connective tissue on the right side in the 37 mm *H. retardatus*. A hypoglossal foramen in the occipital arch is not recognizable in the 27 mm *H. retardatus*, but it is present on the left side in the 37 mm form, as a minute structure which transmits a delicate hypoglossal nerve composed of a ventral root only (figure 51, plate 7).
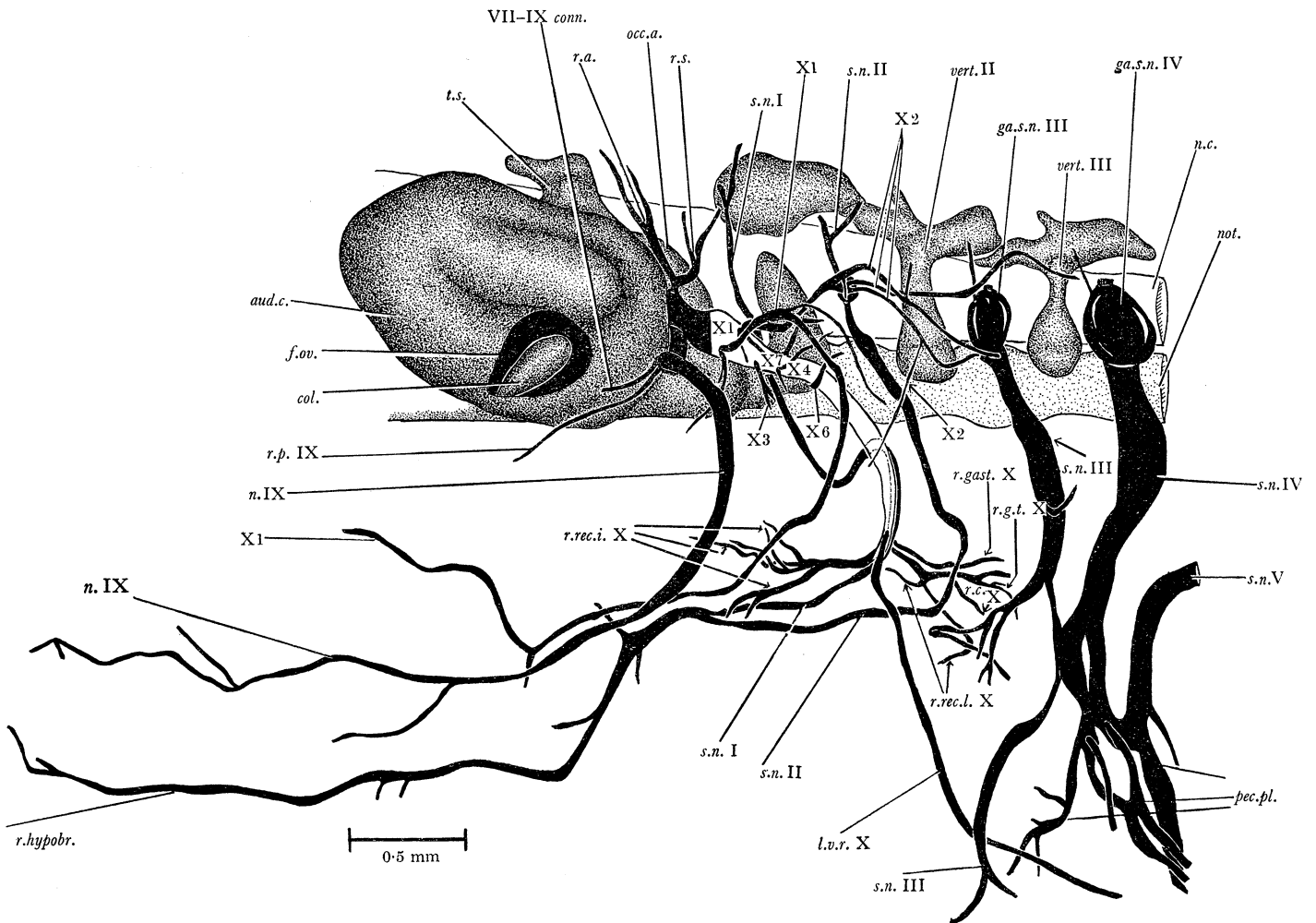
FIGURE 29. 32 mm stage *H. nebulosus*. Lateral reconstruction of the glossopharyngeal, vagus, truncus-intestino-accessorius and anterior spinal nerves.

Meckel's cartilage and the hyobranchial skeleton, apart from differences in size, are similar in the *nebulosus* and *retardatus* specimens. Separation of the hyoid into cerato and hypohyale is suggested in the 27 mm *retardatus*, which division is patent in the 37 mm animal.

The arytenoid cartilages alone (360 μ long) are present at 27 mm (figure 56, plate 7). In the 37 mm stage both arytenoids (540 μ long) and tracheal cartilages (420 μ long) are recognized. A 5th vestigial cleft behind the 4th functional gill cleft (8th head-pharynx segment) is present on both sides in the *H. retardatus* specimens. Furthermore, a 7th pair of vestigial clefts (10th head-pharynx segment) is recognized in the 37 mm specimen, and
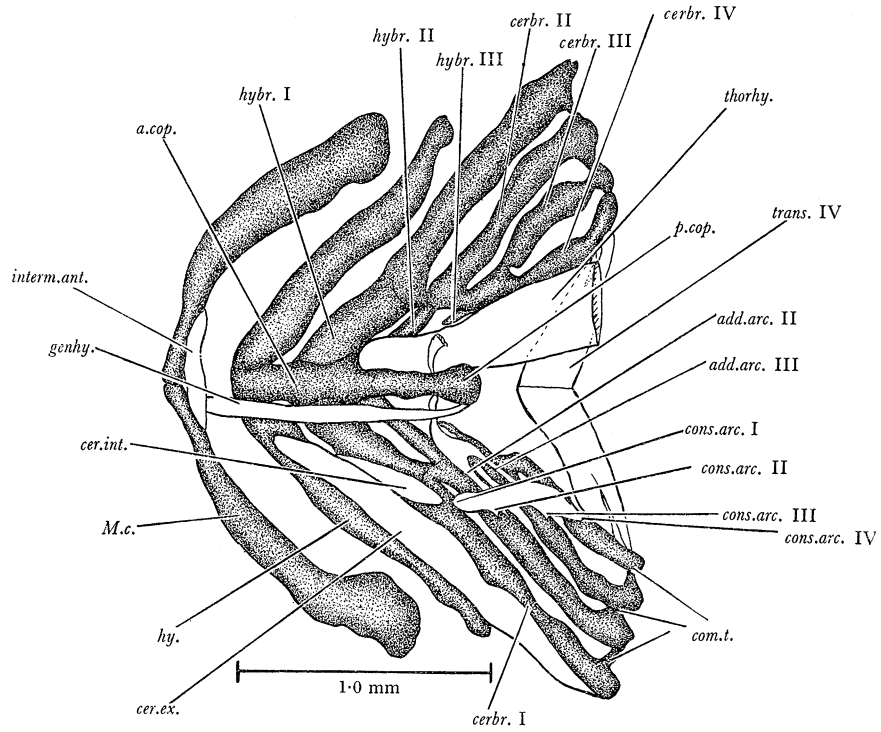
FIGURE 30. 14 mm stage *H. nebulosus*. Ventral reconstruction of the jaws, hyobranchial skeleton and ventral musculature.

FIGURE 31. 17 mm stage *H. nebulosus*. Ventral reconstruction of the jaws, hyobranchial skeleton and ventral musculature.

the arytenoid is situated mesial to this structure (figures 52, 53, 54, 56, plate 7). Paired vestigial 5th external gill filaments are present in both *H. retardatus* specimens.

Joints have developed between the upper anterior and posterior lateral surfaces of adjacent vertebrae. The first vertebra is complete, differing from that of the 32 mm *H. nebulosus* which is deficient in cartilage laterally. There are no ribs associated with the

FIGURE 32. 22 mm stage *H. nebulosus.* Ventral reconstruction of the jaws, hyobranchial skeleton and ventral musculature.

first vertebra, but on the left side of the 37 mm specimen tubercular and capitular cartilaginous processes alone are fused to the lateral base of the neural arch, and the cartilage lateral to the notochord (centrum) respectively. The second vertebra has ribs each with a cartilaginous tubercular and capitular process, but the latter on the left side of the 27 mm specimen is not fused with the notochord. The third vertebra possesses ribs with fused tubercular processes but no capitular ones on the left side in both specimens; both processes are present, however, on the right. The fourth vertebra has ribs with tubercular processes

alone, except on the left side of the 27 mm specimen, where a short unjoined capitular process is recognizable. In both specimens spinal nerve I possesses a ventral root only. Spinal nerves II, III and IV on both sides each possess a dorsal and ventral root and a ganglion.
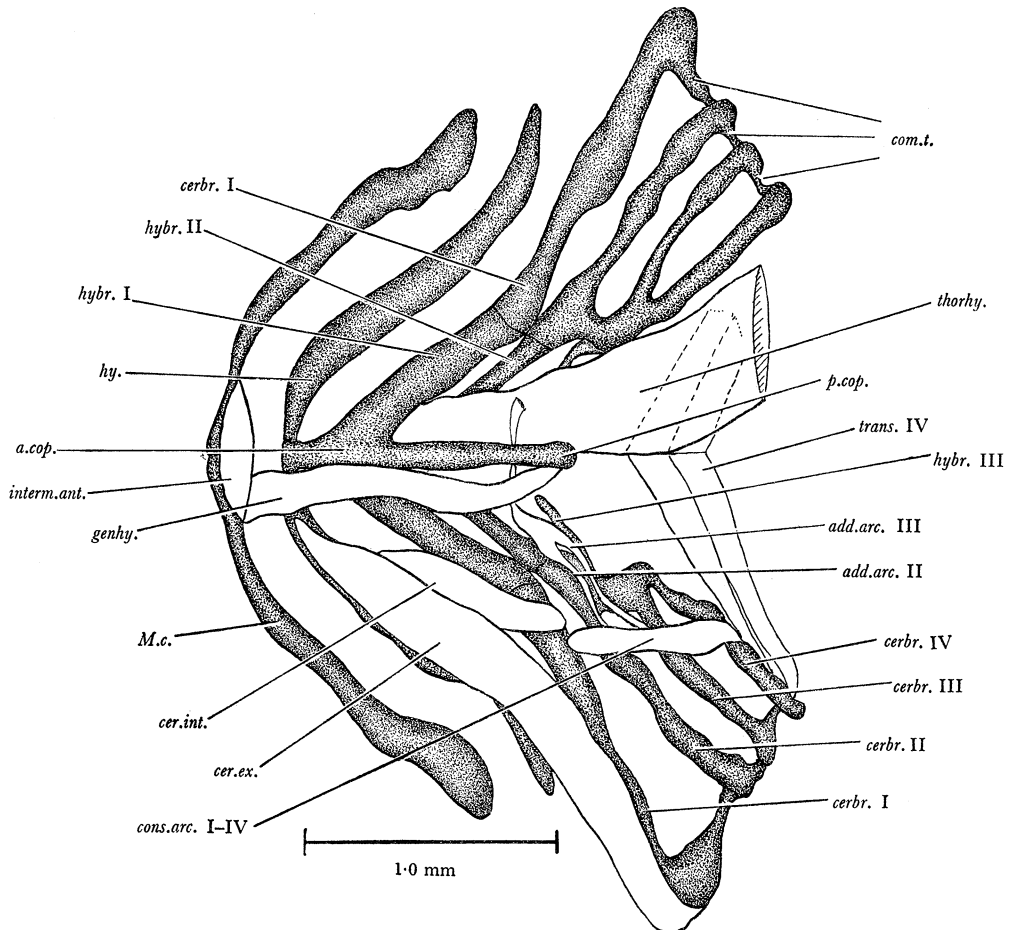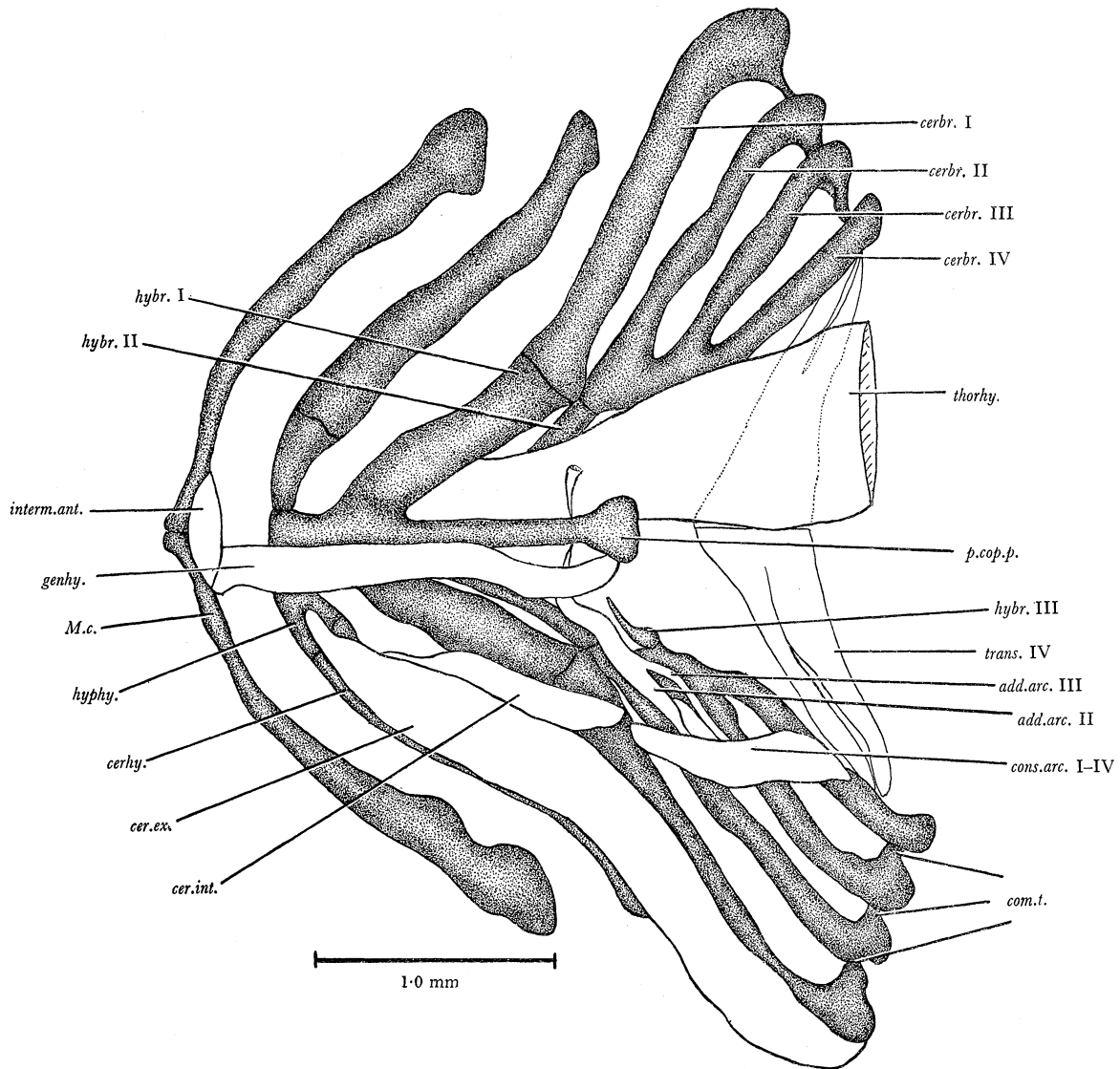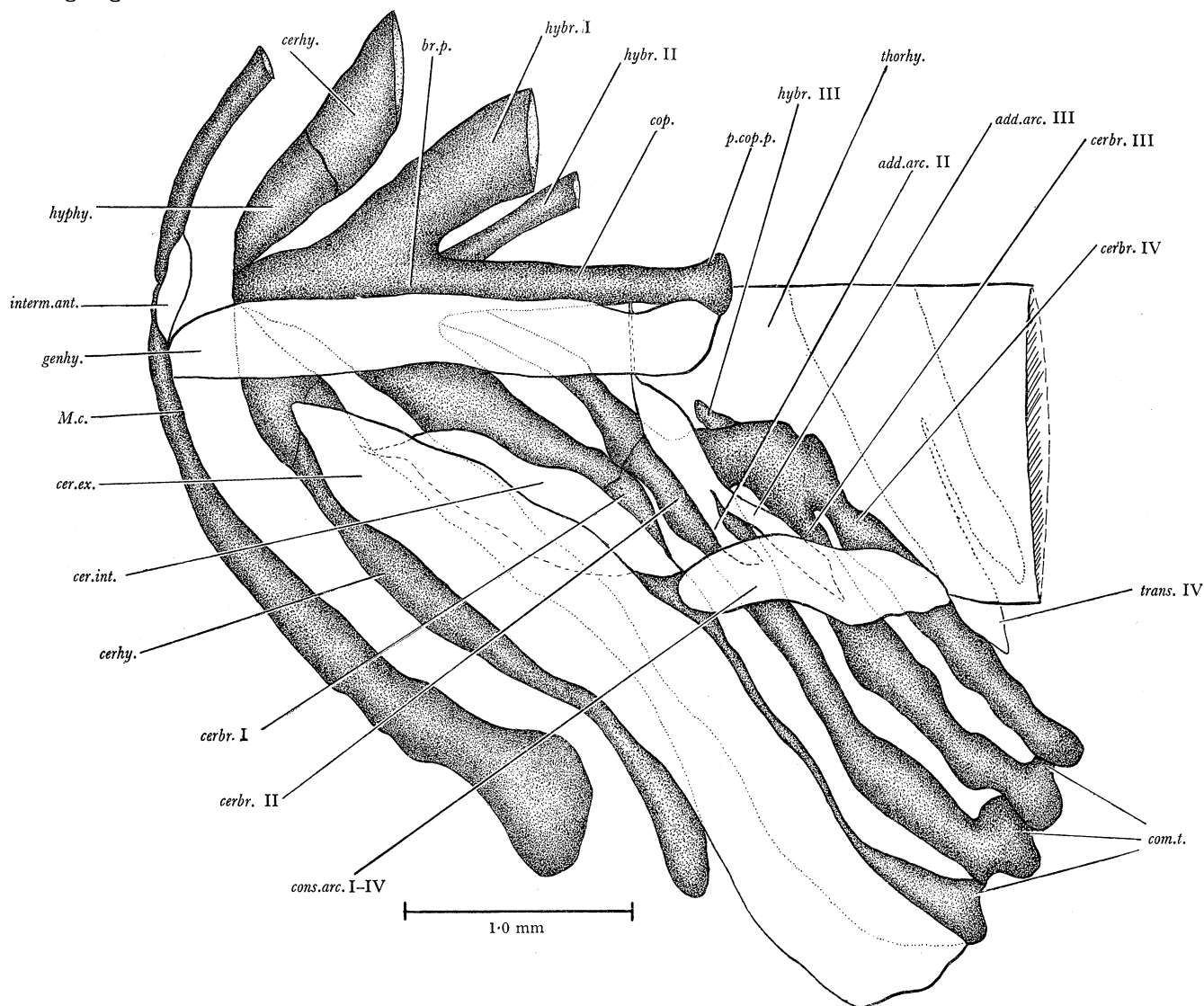

FIGURE 33. 32 mm stage *H. nebulosus*. Ventral reconstruction of a portion of the jaws, hyobranchial skeleton and ventral musculature.

An analysis of the levatores, dilator laryngeus and trapezius muscles in *H. retardatus* reveals a close agreement with the results obtained for *H. nebulosus*. On the left side of the 27 mm stage and the right in the 37 mm animal, the six levator muscle components, followed by the dilator and trapezius muscles are clearly apparent (figure 52, plate 7). The levators in the 37 mm *H. retardatus* are, however, arranged more horizontally than are those of the *H. nebulosus* group. Separate components, apart from the dilator laryngeus and trapezius, are not clearly recognizable on the other sides; the deformation being perhaps the result of preparation, as previously mentioned. In both animals levator I is completely separate along its length. The other levators are more or less fused dorsally with each

other, and they separate into individual components behind. Levators IV, V and VI fuse again to insert on the top of branchiale IV. The rest of the head musculature agrees with the description given for *H. nebulosus*.

Nerve IX is identical with that in *H. nebulosus*. The arrangement of the vagus nerves is complex, and the segmental pattern of the one-to-one muscle-nerve unit is substantially disturbed. This complexity is the result of shortening of the vagus ganglion in the antero-posterior plane, and the fusion of some of the vagus nerve roots. Vagus nerves I, II and III arise from the vagus ganglion at about the same level but separate almost immediately. In both *H. retardatus* specimens vagus I is composed of pre-, post-trematic and pharyngeal rami. The r. post-trematic I innervates levator II and thence leads forwards lateral to branchiale II. Further divisions lead backwards to the muscles in the external gill filaments I and II. Vagus II possesses pre-, post-trematic and pharyngeal rami. After the r. post-trematic II has innervated levator III it leads forwards lateral to branchiale III. In the 27 mm stage further divisions from r. post-trematicus II lead behind to the muscles in gill filaments II and III, and in the 37 mm stage vagus post-trematic nerves II and III fuse along their course, the resulting complex yielding at least six divisions leading posteriorly to the musculature of gill filaments II and III. Vagus III innervates levator IV; in the 27 mm specimen three branches lead from the latter nerve to the gill filament III muscles. Vagus IV of the 27 mm specimen innervates levator V; furthermore it appears to send off a division to levator IV also. Vagus V and VI of the 27 mm stage arise by a common root; an outer division leads to the mesial surface of levator VI, at the junction of the latter with levatores IV and V, and an inner division leads to the dilator laryngeus. In the 37 mm stage vagus IV,V and VI appear to arise from a common root which divides into three, each to innervate levatores V, VI and the dilator laryngeus respectively. The trapezius in both cases is innervated by a stout nerve from the upper surface of the vagus ganglion as in *H. nebulosus*. Thus only nerve IX and vagus nerves I and II curve forwards lateral to branchiale I, II and III, exactly as in *H. nebulosus* and *Cryptobranchus japonicus* larvae (Fox 1954, p. 282). During development there has either been fusion of vagus nerves IV, V and VI or vagus V and VI are lost. The condition of close association of the separate vagus nerves I, II and III, and consideration of the arrangement and muscle innervation of vagus IV, V and VI in both specimens of *H. retardatus* militates against the latter view and encourages the belief that all the nerves are extant.

DISCUSSION

A comparison between the organization of the cranial nerves of *Hynobius* and other urodele larvae reveals a strong similarity when allowance is made for individual variability (Coghill 1902, 1906), and differences in stages of development. The arrangement of the branchial nerves is similar to that in *Cryptobranchus* larvae. The r. ophthalmicus profundus V of *Hynobius* typically divides into three, i.e. r. nasalis internus, externus and palatine profundus. There is also a deep profundus-truncus infraorbitalis anastomosis (Norris 1913), and an association of the truncus (buccalis and maxillaris fibres) with the profundus-palatine anastomosis, mesial to the nasal sac. The arrangement of the profundus clearly agrees with the known similarity of crossopterygian porolepiformes and urodeles. In both groups the nerve is strongly developed and supplies the rostral, dorsal and lateral snout

region; the r. maxillaris V has a weak forward development and terminates near the anterior ventro-lateral corner of the orbit (Jarvik 1942). Further, there is an absence of large blood vessels to the posterior latero-ventral parts of the ethmoid region; they are mainly mesial to the nasal sac. These features differ completely from all other recent vertebrate groups, i.e. elasmobranchs, brachiopterygians, actinopterygians, Dipnoi and Anura, where the profundus is weakly developed, the lateral parts of the snout are innervated by a strongly developed r. maxillaris V and supplied and drained by large blood vessels (Jarvik 1942).

The failure in this work to confirm the presence of a completely chondrified processus pterygoideus confluent with the trabecula (Edgeworth 1923 a), at any stage of *H. nebulosus* or *retardatus* would appear to be a serious disagreement. However, *Cryptobranchus* species certainly possess a hypoglossal foramen, yet in a 37 mm *C. alleghaniensis* in my possession it was not recognizable. Thus quite profound variability in skeletal structures may occur within a species, and absence in a particular case is no proof that the structure never exists. The arrangement of the chondrocranium, pterygo-quadrate cartilage, otic, ascending and basal processes (including the syndesmotic joint), lower jaw, hypobranchial skeleton and copula are all in general agreement with descriptions of previous workers. The presence of a hypoglossal foramen in the occipital crest in *H. nebulosus* like that of *Cryptobranchus* has been described (Fox 1957). Its discovery in the 37 mm *H. retardatus* is thus not unexpected.

A cartilaginous continuity between the columella stilus and the quadrate cartilage is found in many urodeles. It is present in the adult *Onychodactylus* (Okajima 1908; Okutomi 1936); and a synchondrotic connexion was reported by Ryke (1950). In *Cryptobranchus japonicus* 31 mm long 'Der Columellastiel hat in diesem Stadium eine kontinuierliche Verbindung mit dem Proc. oticus des Palatoquadratum', but at 43 mm this connexion was not found: 'Es ist eine Strecke weit von Letzteron getrennt' (Aoyama 1930). The connexion was reported in later stages in the same animal (Miyawaki 1929). The columella stilus is fused with the quadrate cartilage in a 35 mm *H. nebulosus* (Okajima 1911 b), which agrees with my results, a 52 mm *Salamandra maculosa* (Stadtmüller 1924), and there is an attachment in the adult *Amphiuma* (Thyng 1906, pl. 40, fig. 4), *Hynobius*, *Salamandrella* and *Ranodon* (Wiedersheim 1877) and *Ichthyophis glutinosus* (Peter 1898; Thyng 1906). In *Hypogeophis* a backwardly directed otic process (columellar process) temporarily fuses with the columella stilus (de Beer 1937, p. 196). Kingsbury (1903) and Kingsbury & Reed (1908) in various larval urodeles, i.e. *Necturus*, *Spelerpes*, *Desmognathus*, *Amphiuma*, *Ambystoma* and *Proteus* emphasize the primary connexion of the columella to the squamosal; they considered the columella-quadrate cartilage connexion a secondary one. In 28 and 33 mm specimens of *Eurycea bislineata* in my possession, the anterior end of the columella continues forwards as a strand of darkly staining cells which inserts on the squamosal. The quadrate cartilage is situated 260 μ in front of the columella and entirely separate from it. A 26 mm *Cryptobranchus japonicus* has a columella alongside the fenestra vestibuli, over the facial nerve, ending in front as procartilaginous tissue mesially to the incipient squamosal. The distance separating the columella from the quadrate cartilage on both sides is about 80 μ; 40 to 50 μ in the 30 and 32 mm specimens. A common blastematous region unites these structures against the inner surface of the squamosal. The condition is similar in a

37 mm *C. alleghaniensis* where the columella ends against a small hook-like internal squamosal process 50 μ behind the quadrate cartilage. Complete cartilaginous continuity between the columella stilus and quadrate cartilage exists in the 32 mm *H. nebulosus*. Further, just as Kingsbury & Reed (1909) suggest that the ligament hyo-columellare is a secondary development from an originally common blastema of columella and hyoid, so the ligament suspensorio-columellare (inserting on the squamosal earlier and the quadrate later in many urodeles) may be a secondary reduction and insertion, and the primary condition is one of a columella stilus in cartilaginous continuity with the quadrate cartilage. In urodeles (and also other amphibia) the operculum, which appears later in ontogeny, develops from the auditory capsule wall (Dunn 1941), but the columella and stilus are of extra-otic origin (Killian 1890; Platt 1897; Kingsbury & Reed 1909; Reed 1920; Schmalhausen 1923; Okutomi 1936). The belief that the columella is derived from the hyoid from evidence of comparative anatomy has some support from ontogeny. There is cellular continuity between the columella and ceratohyale during larval development in *Necturus*, *Ambystoma* and *Plethodon*, which suggests that these elements may chondrify out of a common blastema (Kingsbury & Reed 1909). In *Hypogeophis* the rudiment of the columella at an early stage is in blastematous continuity with the hyoid (Marcus 1910), the only case of such continuity in an amphibian (Goodrich 1930). If the columella is in fact the top of the hyoid (Gazagnaire 1932; de Beer 1937, p. 412), then the evidence from *Hypogeophis* and *Hynobius* larvae suggests an ancestral cartilaginous continuity between the hyoid and pterygo-quadrate cartilage, similar to the commissura terminales (Gaupp 1904) which join the dorsal ends of the branchiale. The ligaments hyo-columellare and suspensorio-columellare would thus be secondary formations. An ancestral cartilaginous union of hyoid and quadrate cartilages would further emphasize the branchial segmental homologies of the mandibular, hyoid and branchial arches.

In *Cryptobranchus* larvae eight serially homologous branchial arches were demonstrated behind the hyoid; levators I–VI, dilator laryngeus and trapezius were considered to be homologous gill arch muscles, each one innervated by nerves IX and vagus I–VII respectively (Fox 1954). The unrecognized components of this segmental series of arches, i.e. branchiale V–VIII and gill clefts VII and VIII were considered to be either lost from ontogeny, during the course of phylogeny, or modified. Some of these absent components may arise however in older stages of *Cryptobranchus* not investigated. The analysis of *Hynobius nebulosus* and *retardatus* larvae provided further morphological information which supports, supplements and refines some of the earlier conclusions. Two vestigial gill clefts are developed behind the 4th branchiale in *Menopoma* and *Ellipsoglossa* (Edgeworth 1920), and *Amphiuma* (Kingsley 1892). Drüner (1901–4) reported a vestigial cleft (epithelial connexion between the pharyngeal epithelium and the skin), behind branchiale IV in *Triton* and *Salamandra* larvae, as did Makuschok (1911, 1912) in *Triton* and *Pelobates* larvae. In the 32 mm *H. nebulosus* three pairs of vestigial clefts are present; only the first pair in the 14 mm specimen (consisting of a solid plug of cells) reaches the exterior. The 3rd vestigial cleft (7th branchial cleft) of the 10th head segment is associated with the dilator laryngeus and vagus VI. The only other component to be accounted for in this segment is the cartilaginous branchiale, and the dilator laryngeus is clearly inserted on a cylindrical cartilaginous arytenoid (see Goppert 1894, 1898). Wilder (1892) and Gegenbaur (1892)

independently but simultaneously postulated that the cartilago lateralis was the homologue of the 5th branchial bar of fishes. Credence was given to this view by Goppert (1898), Gadow (1901), Gaupp (1904), Versluys (1912) and Goodrich (1930) among others, although homology was denied by Edgeworth (1920, 1935). Normally no 5th branchiale develops in any urodele, but a small one is present in the larval *Hypogeophis* (Gehwolf 1923) which also possesses a cartilaginous laryngo-tracheal skeleton. Thus the latter cannot possibly be a 5th branchial bar as earlier workers supposed. Drüner (1901-4) found a levator V in *Triton* larvae, and he believed that there was at least one branchial segment behind the 4th, between this and the dorsolaryngeus muscle. The arytenoid, according to him, was the homologue of the 6th or even more posterior arch. The arytenoid of the 32 mm *H. nebulosus* is situated just behind the suspected vestigial 7th gill cleft, and mesial to the latter in the 37 mm *H. retardatus*, in a position expected for a branchial bar. The dilator laryngeus which is homologous with the other levators (Wilder 1892, 1896; Goppert 1894, 1898) and is the levator VII (Fox 1954), is innervated by vagus VI and inserts on the arytenoid. Hence it is extremely probable that the arytenoid is the homologue of the 7th branchiale bar of head segment 10, adapted to support the larynx in an air-breathing tetrapod. Disagreement with the views of Gegenbaur and Wilder is a numerical one; they considered the laryngo-tracheal cartilage to belong to head segment 8 (including the pre-mandibular segment). Wilder (1892) first thought that the laryngo-tracheal skeleton developed as a pars laryngeus (5th branchiale) and the pars trachealis, which is a new formation. Later (1896) he accepted Gegenbaur's view (1892) that the cartilago lateralis of *Salamandra* divides into the pars laryngeus and trachealis, the earliest stage corresponding to *Proteus* being the ancestral one. Thus the tracheal cartilage had no independent formation. However in *Hynobius* the tracheal cartilage arises as a separate chondrified cylindrical rod behind the arytenoid, associated with the trapezius (levator VIII) and vagus VII. It lies alongside the tracheal region of the lungs, the latter considered to be homologous with the anterior gill pouches (Makuschok 1911, 1912; Weber & Buvignier 1903). If the origin of the tracheal cartilage is distinct and separate from the arytenoid (Drüner 1901, 1904) and which appears to be the case in the development of *Hynobius*, then the tracheal cartilage may be the homologue of the 8th branchiale of the 11th head segment. The lungs would be related to head segment 11, not segment 10 as I earlier tentatively considered, or segment 9 which would obtain from the work of Makuschok (1911, 1912). The trapezius has therefore lost an original insertion on branchiale VIII in furtherance of other activities associated with the post-pharyngo-pectoral region. No trace of the branchiale VI (head segment 9) exists in urodeles, but Gehwolf (1923) in *Hypogeophis* considered that this was represented by the pararytenoid cartilage, his cartilago lateralis being the homologue of branchiale VII (10th head segment).

In front of the levator I is the large digastricus. Can the muscle be related to the hyoid segment and serially homologized with the levator muscles? If so it should arise in the hyoid segment, be situated in sequence with the levators, innervated by the facialis, and inserted on the hyoid. The digastricus certainly fulfils the first three criteria; furthermore in *Triton* larvae it arises in the hyoid segment and grows forwards to insert on the hind end of Meckel's cartilage. A portion of the deeper fibres is attached to the hyoid, and this region is considered the homologue of the levators (Litzelmann 1923). In the larvae of

Hynobius nebulosus and *retardatus* and *Cryptobranchus japonicus* and *alleghaniensis* there is an insertion on the hyoid as well as Meckel's cartilage, and in the 19 mm *C. japonicus* and the 11·5 mm *H. nebulosus* it arises in the hyoid segment. Wilder (1892) reported the change of insertion of the digastricus from segment 2 to 1 (segments 3 and 2 when the premandibular is included), as did Edgeworth (1925, 1935), and Drüner (1901) recognized its secondary relationship to the lower jaw and its homology with the levator muscles. Recently Schmalhausen (1955) recognized that the amphibian depressor mandibulae develops from the dorsal rudiment of the hyoid musculature through a transitional stage of a functional levator hyoid muscle, and Eaton (1936 a) referred to it as the levator of the hyoid. It is thus extremely likely that some or all of the digastricus is serially homologous with the other levators; that it is a levator hyoideus muscle of the 3rd head segment, but with the origin of jaws it enlarges and secondarily inserts on Meckel's cartilage, to act in reciprocal relationship with the masseter. The related hyoidean or spiracular cleft is an open and functional gill cleft in the ostracoderms (Stensiö 1927; Watson 1954) and acanthodians (Watson 1951); it is an open spiracle in the sharks, rays and some teleosts; open dorsally for a short time but closed later in the larval *Ichthyophis glutinosus* (Ramaswami 1943) and *Hypogeophis* (Marcus 1910), but never open in urodeles. In front of the hyoid cleft in ostracoderms (i.e. *Cephalaspis, Kiaeraspis,* etc.) there are two segments each with a functional gill cleft (Stensiö 1927; Watson 1954). Gnathostomes do not develop functional gill lamellae between the premandibular and mandibular arches, but a vestigial prespiracular gill pouch is present in porolepiform and osteolepiform crossopterygians (Jarvik 1954, p. 91). The second branchial bar (mandibular) of each side becomes the upper and lower jaws; associated with them is the large masseter, situated in sequence with the digastricus and other levator muscles. The masseter is innervated by the trigeminus nerve of the mandibular segment, and inserted on the quadrate and Meckel's cartilages. It would thus seem to possess the requirements of a second head segment levator gill arch muscle, and all or part may thus be serially homologous with the other levators. The levator muscle associated with the premandibular segment could not be recognized in the *Hynobius* head. It may have disappeared completely from ontogeny during the course of evolution, or alternatively it may now be part of the masseter, having changed its insertion (like the digastricus) to insert on Meckel's cartilage. No support for this latter view is supplied from ontogenetic study, and innervation of some constituent of the masseter, by the profundus, would be necessary to support this opinion. Recently, however, Jarvik (1954, p. 100) concluded that the premandibular segment possessed a dorsal preorbital muscle group serially homologous with the muscles of the mandibular and hyoid arches, etc. This muscle is innervated by the r. maxillaris V which he interpreted as the branchial nerve of the premandibular segment. As the levator bulbi musculature arises from this rudiment (Jarvik 1954, p. 86), the levator bulbi would be serially homologous with the other gill arch muscles, i.e. masseter, digastricus, levatores arcuum branchialum, etc. The accompanying table summarizes the segmental arrangement of the various components of the head in *Hynobius.*

Analysis of the development of the head and pharynx of the two most primitive living urodeles (*Hynobius* and *Cryptobranchus*) encourages the belief that the vertebrates originated from an ancestral architype whose head and pharynx at some developmental stage was

composed of eleven functional branchial segments. The adult ostracoderms, e.g. cephalaspids, though highly ossified and intensely specialized, preserved this ancestral numerical arrangement, but even at this early stage the pteraspidomorphs, e.g. *Anglaspis*, probably ceased to possess a functional profundus gill cleft (Watson 1954). Furthermore there is some doubt as to whether there were ten or eleven functional gill clefts in the cephalaspids. If the lungs did indeed originate from the 11th branchial pouches which failed to break through to the exterior, then they must have originated extremely early in vertebrate

TABLE 2. VARIOUS COMPONENTS, PRESENT AT SOME STAGE IN THE ONTOGENY OF *H. NEBULOSUS* LARVAE, AND THEIR RELATIONSHIP TO THE SEGMENTAL PATTERN OF THE HEAD AND PHARYNX

head segment	nerve	muscle	cartilage	gill slit	ext. gill filament
1	profundus	?	trabecula	—	—
2	trigeminus	masseter (lev. mandibulae)	pterygo-quad.- Meckel's cartilage	—	—
3	facialis	digastricus (dep. mandibulae)	hyoid	blind cleft	operculum
4	Glossopharyngeus IX. post-trematic pharyngeus	lev. a. br. I	branchiale I	open cleft	gill fil. I
5	X. v. br. n. I pretrematic post-trematic pharyngeus	lev. a. br. II	branchiale II	open cleft	gill fil. II
6	X. v. br. n. II pretrematic post-trematic pharyngeus	lev. a. br. III	branchiale III	open cleft	gill fil. III
7	X. v. br. n. III pretrematic post-trematic pharyngeus	lev. a. br. IV	branchiale IV	open cleft	gill fil. IV
8	X. v. br. n. IV pretrematic post-trematic	lev. a. br. V	—	vestigial cleft	vestigial gill fil. V
9	X. v. br. n. V post-trematic	lev. a. br. VI	—	vestigial cleft	—
10	X. v. br. n. VI post-trematic	lev. a. br. VII (dilator laryngeus)	arytenoid (p. laryngeus)	vestigial cleft	—
11	X. v. br. n. VII post-trematic	lev. a. br. VIII (trapezius)	tracheal cartilage (p. trachealis)?	lung?	—

phylogeny, as the majority of cephalaspids have ten branchial fossae (Stensiö 1927, p. 150). The evolution of Gnathostomes was accompanied by profound changes at each end of the head and pharynx. In front the jaws arose out of pre-existing skeletogenous (mandibular) branchial bars of the 2nd head segment. The premandibular bars, of the 1st segment, became incorporated into the skull as trabeculae. These changes accompanied the loss of the first two functional gill clefts. Behind there is a gradual regression of pharyngeal components. Thus the adult Teleostomes possess four to five branchial bars; Holocephali, Dipnoi, Batoidea and Selachii have five, although *Chlamydoselachus*, *Hexanchus* and *Pliotrema* have six, and *Heptanchus* seven. The latter also possesses a rudimentary

8th bar and there is a gill cleft between the latter and the 7th (Edgeworth 1935). *Petro-myzon* has seven gill slits and branchial cartilages behind the hyoid (de Beer 1937). The possession of six to fourteen gill slits in the living *Bdellostoma* and twelve to fifteen in the anaspid *Pharyngolepis* (Kiaer 1924) is probably a secondary development. The larval *Hypogeophis* retains a temporary fifth bar, and in urodele and anuran larvae there are four only, except for the exceptional occurrence of an extra pair of branchiale V in *Pleurodeles waltlii* larvae (Signoret 1956). Phylogenetically within the urodele group there is a trend towards a reduction of branchial components, and most plethodonts and *Necturus* and *Proteus* never develop more than three branchiale (Hilton 1947). The ontogenetic reduction of branchial structures in urodeles has been discussed (see above). Thus phylogeny and ontogeny simulate each other in pharyngeal reduction. In the process of terrestrial adaptation by tetrapods pharyngeal reduction continued with the effect that adults never possess open gill clefts, except in *Menopoma*, *Amphiuma*, Proteidae and Sirenidae, which have become readapted to aquatic life. All gills are lost in Amniotes: the slits may open for a short while in reptiles and birds but not at all in most mammals (Goodrich 1930, p. 501). Vestiges of ancestral pharyngeal structures remain during the ontogeny of *Hynobius* and *Cryptobranchus*, but with the subtle and elegant economy which nature regularly practises, components which served for an aquatic existence are used by tetrapods to survive and flourish on land.

SUMMARY

1. A study was made of the development of the head and pharynx of *Hynobius nebulosus* (11·5 to 32 mm long) and *retardatus* (27 and 37 mm long). Reconstructions from the lateral, ventral and dorsal views were prepared from serial transverse sections, by the graphical method.

2. The structure of the chondrocranium, jaws and hyobranchial skeleton (chondrified from the 14 mm stage onwards in *H. nebulosus*) conformed to the general urodele pattern, and in general agreed with previous descriptions. However, a rudimentary fenestra lateralis nasi is found in the nasal capsule of the 32 mm *H. nebulosus*, hitherto not reported in this species, and in no stage of the latter or of *H. retardatus* was a completely chondrified processus pterygoideus represented. The result fails to confirm Edgeworth's (1923 a) description of a completely chondrified process, confluent with the trabeculae cranii and the inner margin of the lamina orbito-nasalis, in a 20 mm *H. nebulosus*.

3. A syndesmotic joint in the basal process of the two species is recognized and this is in accord with earlier descriptions.

4. The occipital crest of the 22 and 32 mm *H. nebulosus* larvae possesses a hypoglossal foramen hitherto only found in *Cryptobranchus* among living amphibia (see Fox 1957). This foramen (with a ventral hypoglossal nerve which emerges through it) is also present on one side in the 37 mm *H. retardatus*. The structure of the occipital crest and its segmental relationship with the neural arches further supports the belief of its neural arch homology.

5. The columella stilus is confluent with the back of the pterygo-quadrate cartilage in the 32 mm *H. nebulosus* which confirms Okajima's (1911 b) description of a 35 mm larva of the same species. As the columella and hyoid originate from a common blastema in *Hypogeophis* larvae (Marcus 1910) and because of the presence of the cartilaginous con-

tinuum of the columella and quadrate cartilage in *H. nebulosus*, it is suggested that there was an ancestral cartilaginous connexion between the hyoid and pterygo-quadrate cartilages, similar to the commissura terminales which unite the dorsal ends of the branchiale. This feature would further emphasize the branchial segmental homologies of the mandibular, hyoid and branchial cartilages.

6. A separate angulare bone is present in the lower jaw, which confirms the description of previous workers. The origin and relationship of the exoccipitals to the bracing ossifications of the neural arches leads to the conclusion that the former are neural in origin and incorporated into the skull.

7. The pattern of the peripheral cranial nerves is similar to that in other urodele larvae when allowance is made for individual variability and different relative stages of development. The r. ophthalmicus profundus is strongly developed and supplies the rostral, dorsal and lateral snout regions in contrast to the weak forward development of the r. maxillaris V. The arrangement lends support to the view of the separate origin of the urodeles from Crossopterygian Porolepiformes (Jarvik 1942).

8. The structure and arrangement of the branchial components of *Hynobius* larvae is similar to the condition in *Cryptobranchus* larvae, and there is a segmental series of eleven head segments. Each of the eight post-hyoid segments is composed of a levator muscle, concomitant nerve (IX and vagus I–VII), branchiale and gill cleft, but no traces of branchiale V and VI are recognizable. Behind the 4th functional gill cleft are three vestigial blind ones, and then the larynx and trachea leading to the lungs. Levators IV, V and VI are joined ventrally, and owing to the loss of branchiale V and VI are secondarily inserted on the top of branchiale IV. The dilator laryngeus and trapezius are considered to be the homologues of levators VII and VIII, and the arytenoid and tracheal cartilages are branchiale VII and VIII, of the tenth and eleventh head-pharynx segments. This conclusion agrees with the views of Gegenbaur and Wilder, that the laryngo-tracheal skeleton is homologous with a branchial bar, but disagrees in that it is not the 5th branchiale of head segment 8. The lungs are considered to have developed from gill pouches of the eleventh segment, which failed to break through to the exterior extremely early in vertebrate evolution.

9. The digastricus belongs to the hyoidean or third head segment and is serially homologous with the other levator gill arch muscles. Its insertion on the back of Meckel's cartilage is a secondary one to depress the lower jaw. In *Hynobius* larvae the muscle has a dual insertion; a primary one on the hyoid in addition to that on Meckel's cartilage.

10. It is suggested that all or part of the masseter is a mandibular gill arch muscle, serially homologous with the digastricus and levator muscles.

11. The basic pattern of the head and pharynx is modified in ontogeny by omission, distortion or addition to the various segmental components, to a greater or lesser degree within different groups of vertebrates.

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REFERENCES

Aoyama, F. 1930 Die Entwicklungsgeschichte des Kopfskelettes des *Cryptobranchus japonicus*. *Z. Anat. EntwickGesch.* **93**, 107–181.

Bogoljubsky, S. N. 1925 Morphologie des hyoid-apparatus bei den Amphibien. III. Teil. *Rev. zool. russe*, **5**, 3–25.

Chung, I. 1929 Über die morphologischen Studien der Nasenregion bei den Urodelen. I. Beiträge zur Morphologie des Narialen bei den japanischen Urodelen. *Acta med. Keijo*, **12**, 81–97.

Chung, I. 1931 Morphologische Studien über die Nasenregion der Urodelen. IV. Über das knorpelige Nasenskelett der japanischen Urodelen. *Keijo J. Med.* **2**, 368–381.

Chung, I. 1932 Morphologische Studien über die Nasenregion der Urodelen. V. Beiträge zur Entwicklungsgeschichte des knorpeligen und knöchernen Nasenskelettes bei *Hynobius leechii*. *Keijo J. Med.*, **3**, 341–353.

Chung, I. & Yatabe, T. 1931 Morphologische Studien über die Nasenregion bei den Urodelen. II. Über das knocherne Nasenskelett bei den japanischen Urodelen. *Keijo J. Med.* **2**, 254–271.

Coghill, G. E. 1902 The cranial nerves of *Amblystoma tigrinum*. *J. comp. Neurol.* **12**, 205–289.

Coghill, G. E. 1906 The cranial nerves of *Triton taeniatus*. *J. comp. Neurol.* **16**, 247–264.

de Beer, G. R. 1926 The orbito-temporal region of the skull. *Quart. J. micr. Sci.* **70**, 263–370.

de Beer, G. R. 1937 *The development of the vertebrate skull.* Oxford University Press.

de Villiers, C. G. S. 1936 Some aspects of the amphibian suspensorium. *Anat. Anz.* **81**, 225–247.

Drüner, L. 1901 Studien zur Anatomie der Zungenbein, Kiemenbogen und Kehlkopfmuskeln der Urodelen. *Zool. Jb. Anat.* **15**, 435–622.

Drüner, L. 1904 Studien der Anatomie der Zungenbein, Kiemenbogen und Kehlkopfmuskeln der Urodelen. II. Theil. *Zool. Jb. Anat.* **19**, 361–690.

Dunn, E. R. 1922 Sound transmitting apparatus of salamanders and the physiology of the Caudata. *Amer. Nat.* **16**, 418–427.

Dunn, E. R. 1923 The salamanders of the family Hynobiidae. *Proc. Amer. Acad. Arts Sci.* **58**, 445–523.

Dunn, E. R. 1941 The opercularis muscle of salamanders. *J. Morph.* **69**, 207–215.

Eaton, T. H. 1936a The myology of salamanders with particular reference to *Dicamptodon ensatus* (Eschscholtz). I. Muscles of the head. *J. Morph.* **60**, 31–75.

Eaton, T. H. 1936b The gularis muscle in Urodela. *J. Morph.* **60**, 317–324.

Edgeworth, F. H. 1920 On the development of the hyobranchial and laryngeal muscles in the Amphibia. *J. Anat., Lond.* **54**, 125–162.

Edgeworth, F. H. 1923a On the quadrate in *Cryptobranchus*, *Menopoma* and *Hynobius*. *J. Anat., Lond.* **57**, 238–244.

Edgeworth, F. H. 1923b On the larval hyobranchial skeleton and musculature of *Cryptobranchus*, *Menopoma* and *Ellipsoglossa*. *J. Anat., Lond.* **57**, 97–105.

Edgeworth, F. H. 1925 On the autostylism of Dipnoi and Amphibia. *J. Anat., Lond.* **59**, 225–264.

Edgeworth, F. H. 1935 *The cranial muscles of vertebrates.* Cambridge University Press.

Fischer, J. G. 1864 Ueber die Perennibranchiaten und Derotremen. *Anat. Abhandlungen. Erstes Heft.* Hamburg.

Fox, H. 1954 Development of the skull and associated structures in amphibia with special reference to the urodeles. *Trans. Zool. Soc. Lond.* **28**, 241–304.

Fox, H. 1957 The occipital crest and anterior spinal nerves in the larval urodele *Hynobius nebulosus*. *Proc. Zool. Soc. Lond.* **138**, 365–368.

Fukuda, Y. 1928 Zur Morphologie und Entwicklungsgeschichte des Hyobranchialskelettes von *Megalobatrachus japonicus*. *Folia anat. jap.* 6, 327–374.

Gadow, H. 1901 *Amphibia and reptiles*. The Cambridge Natural History. Vol. 8. London.

Gaupp, E. 1904 Das Hyobranchialskelet der Wirbeltiere. *Ergebn. Anat. EntwGesch.* 14, 808–1048.

Gaupp, E. 1906 Die Entwicklung des Kopfskelets. *Hertwig's Handbuch d. Entwicklungs lehre*, 3, Abt. 2, 573–875.

Gaupp, E. 1911 Ueber dem N. Trochlearis der Urodelen und über die Austritts-stellen der Gehirn-nerven aus dem Schädelraum im allgemeinen. *Anat. Anz.* 38, 401–444.

Gazagnaire, C. 1932 Origine de l'oreille chez *Rana temporaria*. *C.R. Soc. Biol., Paris*, 110, 1076–78.

Gegenbaur, C. 1892 Arbeit über die Epiglottis. *Festschr. f. A. v. Koelliker*. Leipzig. 1–69.

Gehwolf, F. 1923 Der Kehlkopf bei *Hypogeophis*. *Z. Anat. EntwickGesch.* 68, 433–454.

Goodrich, E. S. 1911 On the segmentation of the occipital region of the head in the Batrachia Urodela. *Proc. Zool. Soc. Lond.* pp. 101–120.

Goodrich, E. S. 1930 *Studies on the structure and development of vertebrates*. London: Macmillan.

Goppert, E. 1894 Die Kehlkopfmuskulatur der Amphibien. *Morph. Jb.* 22, 1–78.

Goppert, E. 1898 Der Kehlkopf der Amphibien und Reptilien. *Morph. Jb.* 26, 282–329.

Gray, P. 1930 The attachments of the urodele rib to the vertebra, and their homologies with the capitulum and tuberculum of the craniate rib. *Proc. Zool. Soc. Lond.* pp. 907–11.

Higgins, G. M. 1920 The nasal organs in Amphibia. *Illinois biol. Monogr.* 6, no. 1, 7–91.

Hilton, W. A. 1946. Preliminary remarks on the skeletons of the family Hynobiidae. *J. Ent. Zool.* 38, 40–45.

Hilton, W. A. 1947 The hyobranchial apparatus of Salamandridae. *J. Ent. Zool.* 39, 68–72.

Hyrtl, J. 1865 *Cryptobranchus japonicus*. *Schediasma Anat. quod Almae et Antiquissimae*. Univ. Vindo-bonensi.

Inukai, T. 1932 Urodelarten aus Nordjapan mit besonderer Berücksichtigung der Morphologie des Schädels. *J. Fac. Sci. Hokkaido Univ.* (VI) 1, no. 4, 191–217.

Jarvik, E. 1942 On the structure of the snout of Crossopterygians and lower Gnathostomes in general. *Zool. Bidr. Uppsala*, 21, 235–675.

Jarvik, E. 1954 On the visceral skeleton in *Eusthenopteron* with a discussion of the parasphenoid and palatoquadrate in fishes. *K. Svensk. Vet.-Akad. Handl.*, (4) 5, nr. 1, 3–104.

Kiaer, J. 1924 The Downtonian fauna of Norway. I. Anaspida. *Skr. VidenskSelsk. Kristiania Math. Kl.* 1, no. 6, 1–139.

Killian, G. 1890 Die Ohrmuskeln des Krokodiles nebst vorläufigen Bemerkungen über die Homologie des Musculus stapedius und des Stapes. *Jena Z. Naturw.* 24, 634–654.

Kingsbury, B. F. 1903 The columella auris and nerve facialis in Urodela. *J. comp. Neurol.* 13, 313–334.

Kingsbury, B. F. & Reed, H. D. 1908 The columella auris in the Amphibia. *Anat. Rec.* 2, 81–91.

Kingsbury, B. F. & Reed, H. D. 1909 The columella auris in Amphibia. *J. Morph.* 20, 549–628.

Kingsley, J. S. 1892 The head of an embryo *Amphiuma*. *Amer. Nat.* 26, 671–680.

Kunitomo, K. 1910 Über die Entwicklungsgeschichte des *Hynobius nebulosus*. *Ergebn. Anat. Entw-Gesch.* 40, 193–283.

Kunitomo, K. 1911 Die Kiemblattbildung des *Hynobius nebulosus*. *Ergebn. Anat. EntwGesch.* 44, 457–523.

Lapage, E. O. 1928 The septomaxillary. I. In the Amphibia Urodela. *J. Morph.* 45, 441–471.

Litzelmann, E. 1923 Entwicklungsgeschichtliche und vergleichendanatomische Untersuchungen über den Visceralapparat der Amphibien. *Z. Anat. EntwickGesch.* 67, 457–493.

Low, J. W. 1927 Contributions to the development of the pelvic girdle. II. The pelvic girdle in the batrachian *Hynobius nebulosus* s. *Ellipsoglossa nebulosus*. *Proc. Zool. Soc. Lond.* 2, 865–878.

Luther, A. 1914 Über die vom N. trigeminus versorgte Muskulatur der Amphibien. *Acta Soc. Sci. fenn.* **44**, 1–151.

Makuschok, M. 1911 Zur Frage über die phylogenetische Entwickelung der Lungen bei den Wirbeltieren. *Anat. Anz.* **39**, 1–13.

Makuschok, M. 1912 Zur Frage über die phylogenetische Entwickelung der Lungen bei den Wirbeltieren. *Anat. Anz.* **42**, 59–70.

Marcus, H. 1910 Beiträge zur Kenntnis der Gymnophionen. III. Zur Entwicklungsgeschichte des Kopfes. *Morph. Jb.* **40**, 105–183.

Matthews, J. P. 1950 The cranial musculature of the Asiatic urodele *Onychodactylus japonicus* (Houttuijn). *Ann. Univ. Stellenbosch*, **26**A, 22–44.

Matumoto, K. 1932 Beiträge zur Morphologie und Entwicklung des Hyobranchialskelettes bei *Hynobius leechii*. *Keijo. J. Med.* **3**, 91–112.

Mikamo, K. 1955 The occurrence of *Salamandrella keyserlingii* (Dyb) in Hokkaido. *Annot. zool. jap.* **28**, 44–47.

Miyawaki, S. 1929 Die Entwicklung der Ohrkapsel und des Schalleitenden Apparates von *Megalobatrachus japonicus*. *Folia anat. jap.* **7**, 457–488.

Murayama, T. 1928 Über die Balanzierstange bei *Hynobius* larven. *Folia anat. jap.* **6**, 375–388.

Noble, G. K. 1927 The value of life history data in the study of the evolution of the Amphibia. *Ann. N.Y. Acad. Sci.* **30**, 31–128.

Noble, G. K. 1931 *The biology of the Amphibia.* New York: McGraw-Hill Co. Inc.

Norris, H. W. 1913 The cranial nerves of *Siren lacertina*. *J. Morph.* **24**, 245–338.

Okajima, K. 1908 Die Osteologie des *Onychodactylus japonicus*. *Z. wiss. Zool.* **91**, 351–381.

Okajima, K. 1909 Über des Hyobranchialskelett von *Onychodactylus*. *Anat. Anz.* **34**, 182–185.

Okajima, K. 1911 *a* Über das Vorkommen von zwei Foramina perilymphatica beim Urodelenohr. *Anat. Anz.* **38**, 25–28.

Okajima, K. 1911 *b* Die Entwickelung des Gehörorgans von *Hynobius*. *Ergebn. Anat. EntwGesch.* **45**, 1–80.

Okajima, K. 1922 Zur Anatomie des Hyobranchialskelettes bei den Onychodactyluslarven. *Folia anat. jap.* **1**, 195–200.

Okajima, K. & Tsusaki, T. 1921 Beiträge zur Morphologie des Skleralknorpels bei den Urodelen. *Z. Anat. EntwGesch.* **60**, 631–651.

Okutomi, K. 1936 Die Entwicklung des Kopfskelettes beim japanischen Krallensalamander. *Zool. Jb. Anat.* **61**, 1–44.

Oyama, J. 1930 *a* Some embryological notes of *Hynobius naevius*. *Copeia*, no. 173, 92–94.

Oyama, J. 1930 *b* Balancer in *Diemictylus pyrrhogaster* and in *Hynobius nebulosus*. *Copeia*, no. 173, 103–106.

Parker, W. K. 1882 On the structure and development of the skull in Urodeles. *Trans. Zool. Soc. Lond.* **11**, 171–214.

Penfold, R. L. & Roofe, P. G. 1956 The anatomical study of the neural tube and cranial ganglia of the developmental stages of *Amblystoma maculatum*. *Univ. Kansas Sci. Bull.* **37**, 579–625.

Peter, K. 1898 Die Entwicklung und funktionelle Gestaltung des Schädels von *Ichthyophis glutinosus*. *Morph. Jb.* **25**, 555–628.

Platt, J. 1897 The development of the cartilaginous skull and of the branchial and hypoglossal musculature in *Necturus*. *Morph. Jb.* **25**, 377–464.

Pope, C. H. 1931 Notes on amphibians from Fukien, Hainan, and other parts of China. *Bull. Amer. Mus. nat. Hist.* **6**, 397–610.

Ramaswami, L. S. 1943 The segmentation of the head of *Ichthyophis glutinosus* (L.). *Proc. Zool. Soc. Lond.* **112**B, 105–112.

Reed, H. D. 1920 The morphology of the sound transmitting apparatus in caudate Amphibia, and its phylogenetic significance. *J. Morph.* **33**, 325–387.

Ryke, P. A. J. 1950 Contributions to the cranial morphology of the Asiatic urodele *Onychodactylus japonicus* (Houttuijn). *Ann. Univ. Stellenbosch*, **26**A, 3–21.

Sato, I. 1941 The salamanders of Formosa (text in Japanese). *Trans. nat. hist. Soc. Formosa*, **31**, 114–124.

Schmalhausen, J. J. 1923 Der Suspensorialapparat der Fische und das Problem der Gehörknöchelchen. *Anat. Anz.* **56**, 534–543.

Schmalhausen, J. J. 1954 The development of gills, their blood vessels and gill filament musculature in Amphibia. *Zool. Zh.* **33**, no. 4, 848–868. (*Zool. J. Acad. Sci. U.S.S.R.*)

Schmalhausen, J. J. 1955 Development of the visceral musculature of tailed Amphibia. *Zool. Zh.* **34**, no. 1, 162–174. (*Zool. J. Acad. Sci. U.S.S.R.*)

Schmidt, F. J. J., Goddard, G. J. & van der Hoeven, T. 1864 Anatomie van den *Cryptobranchus japonicus*. *Natuurk. verh. Hollandsche Haarlem 2 verz.* **19**, 1–66.

Shitkov, B. 1895 Über die Fortpflanzung des *Isodactylium schrenki* (Strauch). *Zool. Anz.* **18**, 165–168.

Shitkov, B. 1899 Über den Bau und die Entwicklung des Skelettes der freien Gliedmalsen des *Isodactylium schrenki* (Strauch). *Zool. Anz.* **22**, 246–257.

Signoret, J. 1956 Sur la présence d'un arc branchial supplementaire chez *Pleurodeles waltlii* Michah. *Bull. Soc. zool. Fr.* **81**, 384–386.

Smith, L. 1920 The hybranchial apparatus of *Spelerpes bislineatus*. *J. Morph.* **33**, 527–583.

Stadtmüller, F. 1924 Studien am Urodelen Schädel. I. Zur Entwicklungsgeschichte des Kopfskelettes der *Salamandra maculosa*. *Z. Anat. EntwGesch.* **75**, 149–225.

Stadtmüller, F. 1929*a* Vorweisung. B. Modelle und Preparate vom Kopfskelet asiatischer Salamandriden (*Onychodactylus japonicus* und *Hynobius nebulosus*). *Verh. anat. Ges. Jena*, **38**, 219–220.

Stadtmüller, F. 1929*b* Beobachtungen zur Kenntnis des Scleralknorpels bei Amphibien insbesondere bei gewissen Urodelen. *Morph. Jb.* **61**, 221–254.

Stadtmüller, F. 1936 Kranium und Visceralskelet der Amphibien und Stegocephalen. *Handb. vergl. Anat.* Bolk, Goppert, Kallius, Lubosch., **4**, 501–698.

Stadtmüller, F. 1937 Zur Kenntnis des Angulare (= Reptilien angulare), am Unterkiefer der Landwirbeltiere. *Morph. Jb.* **79**, 436–470.

Stensiö, E. A. 1927 The Downtonian and Devonian vertebrates of Spitzbergen. I. Family Cephalaspidae. *Skr. om. Svalbard og. Nordishavet*, no. 12, pt. 1.

Stohr, P. 1882 Zur Entwicklungsgeschichte der Anurenschädels. *Z. wiss. Zool.* **36**, 68–103.

Sumi, R. 1926 Über die Morphogenese des Gehirns von *Hynobius nebulosus*. *Folia anat. jap.* **4**, 171–270.

Suzuki, S. 1933 Transplantationsversuche der Vorderbeinanlage der Urodelenlarve (*Hynobius nebulosus*) an Anurenlarven (*Bufo vulgaris japonicus* & *Rana japonica* Gunther). *Jap. J. med. Sci.* **4**, 1–60.

Suzuki, S. & Kobayashi, K. 1939 Beiträge zur Schwanzentwicklung der Amphibien (Vorläufige). *Jap. J. med. Sci.* **7**, 211–218.

Tago, K. 1931 *The salamanders of Japan.* Tokio, 1931. (Translation in English from Japanese in British Museum (Nat. Hist.).)

Terry, R. J. 1906 The nasal skeleton of *Ambystoma punctatum*. *Trans. Acad. Sci. St Louis*, **16**, no. 5, 95–124.

Thyng, F. W. 1906 Squamosal bone in tetrapodous vertebrates. *Proc. Bost. Soc. nat. Hist.* **32**, 387–419.

Tsusaki, T. 1922 Zur Morphologie und Entwicklungsgeschichte des Hyobranchialskelettes von *Hynobius*. *Folia anat. jap.* **1**, 1–21.

Temminck, C. J. & Schlegel, H. 1838 *Reptilia*. In Siebold, P. F. von, *Fauna Japonica*. Lugduni Batavorum.

Versluys, J. 1912 *Handworterb. d. Naturwiss.* I. Gustav Fischer, Jena.

Watson, D. M. S. 1951 *Palaeontology and modern biology.* Yale Univ. Press.

Watson, D. M. S. 1954 A consideration of ostracoderms. *Phil. Trans.* B, **238**, 1–25.

Weber, A. & Buvignier, A. 1903 La significance morphologique de l'ebauche pulmonaire chez les vertébrés. *C.R. Soc. Biol., Paris,* **55,** 1396–7.

Wiedersheim, R. 1877 Das Kopfskelet der Urodelen. *Morph. Jb.* **3,** 352–448, 459–548.

Wilder, H. H. 1892 Studies in the phylogenesis of the larynx. *Anat. Anz.* **7,** 570–580.

Wilder, H. H. 1896 The amphibian larynx. *Zool. Jb. Anat.* **9,** 273–318.

Yatabe, T. 1931 Morphologische Studien über die Nasenregion der Urodelen. III. Beiträge zur Kenntnis der Anatomie und Entwicklung des Tränennasengangs bei den japonischen Urodelen. *Keijo J. Med.* **2,** 277–296.

Yatabe, T. 1932 Zur Morphologie des Skleralknorpels. V. Über die Einfluss in Wasser geloster Nährstoffe und die Entwicklung des Skeralknorpels bei *Hynobius leechii. Keijo J. Med.* **3,** 393–402.

a.a.f. anterior auditory fenestra
a.c.c.a. anterior carotis cerebralis artery
a.cop. anterior copula
a.c.v. anterior cardinal vein
add.arc. II, III adductor arcuate muscles II, III
a.e.a. III–IV–V–VI afferent epibranchial
    arteries III–VI
aud.c. auditory capsule
aud.v. auditory vesicle

b.a. artery basalis
bal. V balancer nerve of r. mandibularis V
b.comm. basicapsular commissure
b.m. balancer membrane
br. I, II, III, IV branchiale I–IV
b.r.o.p. V branch of r. ophthalmicus profundus
    V
br.p. branchial plate
b.p. basal plate

cav.i. cavum internasale
cerbr. I, II, III, IV ceratobranchiale I–IV
cer.ex. ceratohyoideus externus
cerhy. ceratohyale
cer.int. ceratohyoideus internus
c.ob. cartilago obliqua
col. columella
col.s. columella stilus
com.t. commissura terminalis
cond. occipital condyle
conn. VII–IX Connective of Willis
cons.arc. I, II, III, IV constrictor arcuate muscles
    I–IV
cop. copula
c.p.i.l. cartilago prenasalis inferior lateralis
c.ret. cartilago retronarina
c.s. crista sellaris
c.t. crista trabecula
c.v. cutaneous vein

d.a. dorsal aorta
d.C. ductus Cuvieri
dig. digastricus
dig.r. branch from VII–IX Conn. to digastricus
d.l. dilator laryngeus
d.p. V deep profundus V

e. eye
e.e.a. III, IV, V, VI efferent epibranchial
    arteries III–VI
e.e.a.h. efferent epibranchial artery associated
    with the hyoid
e.c. ethmoidal column
e.c.a. external carotid artery
e.n. external naris
exocc. exoccipital bone

f.ch. fenestra choanalis
fen.ac.a. & p. fenestra acoustica anterior and
    posterior
fen.end.d. & v. fenestra endolymphatica dorsalis
    and ventralis
fen.per. fenestra perilymphatica
f.g. facialis ganglion
f.hy. foramen hyomandibularis
f.hyg. foramen hypoglossus
f.hyp. foramen hypophyseos
f.j. foramen jugulare
f.lat. fenestra lateralis nasi
f.na. fenestra narina
f.ol. foramen olfactorius
f.on. foramen orbito-nasalis
f.ov. fenestra ovalis
f.p. foramen palatinus
f.po. foramen prootica

ga. V trigeminus ganglion
ga. VII facialis ganglion
ga. IX glossopharyngeal ganglion
ga. X vagus ganglion
ga.s.n. II, III, IV ganglia spinal nerves II, III,
    IV
g.c. I–VII gill clefts I–VII
genhy. geniohyoideus muscle
g.f. I, II, III, IV external gill filaments I–IV
g.g. gasserian ganglion

h.b. hind-brain
h.n. hypoglossal nerve
ht. heart
hy. hyoid
hybr. I, II, III hypobranchiale I, II, III
hy.c. hyoid cleft
hyphy. hypohyale

i.c.a. internal carotid artery
i.l.o.v. inferior lateral orbital vein
inc.p. incisura prootica
interhy. interhyoideus muscle
interm.ant. intermandibularis anterior

l. I–VI levator arcus branchialis I–VI
lat.conn. lateral cartilaginous connexion between
    neural arches
lat.fac. lateralis constituent of facialis ganglion
l.d.a. lateral dorsal aorta
l.f.g. lateralis facialis ganglion
lg. lung
lig.d.a. ligament of dilator laryngeus on arytenoid
l.i.r. X lateralis inferior ramus X
l.m.a. levator mandibulae anterior
l.m.e. levator mandibulae externus

m. mouth cavity
m.b. mid-brain
M.c. Meckel's cartilage
m.fil. external gill filament muscle
m.v. mandibular vein

n. III, IV, V, VII, IX oculomotor, trochlear, trigeminus, facialis and glossopharyngeal nerves
n.a. I, II, III neural arches I, II, III
n.c. nerve cord
n.cap. nasal capsule
n.oss. neural ossification
not. notochord
n.s. nasal sac
n.sp. II, III neural spines II, III
n.v. nasal vein

occ.a. occipital arch
oc.f. oculomotor foramen
oes. oesophagus
o.l. olfactory lobe
o.n. olfactory nerve
op.f. optic foramen
orb.v. orbital vein
o.v. optic vein

p.a. processus ascendens
pal.a. palatine artery
p.ary. arytenoid cartilage
p.b. processus basalis
p.bt. processus basitrabecularis
p.c.c.a. post-carotis cerebralis artery
p.cop. post-copula
p.cop.p. post-copula plate
p.c.s. post-cardinal sinus
p.c.v. post-cerebral vein
pec.pl. pectoral plexus
peric. pericardial cavity
p.f.c. prefacial commissure
p.g. profundus ganglion
phx. pharynx
p.m.a.f. primary medial auditory foramen
p.o. processus oticus
post.z.n.a. II, III post-zygapophysis, neural arch II, III
p.p. pila prootica
p.p.c. post-palatine commissure
p.ptg. processus pterygoideus
p.q.c. pterygo-quadrate cartilage
p.r. prootic recess
pre.z.n.a. II, III prezygapophysis, neural arch II, III
p.t. pars trachealis

r. rib

rect.p. rectus posterior
r.gast. X ramus gastricus X
r.g.t. X ramus gastrotrachealis X
r.h.f. ramus hyomandibularis facialis
r.hypobr. ramus hypobranchialis
r.in. V ramus intermandibularis V
r.in.a. V ramus intermandibularis anteri
r.in.p. V ramus intermandibularis poster
r.int. X ramus intestinalis X
r.j.f. ramus jugularis facialis
r.mand. V ramus mandibularis V
r.mass. V ramus to masseter from r. bularis V
r.max. V ramus maxillaris V
r.m.e.f. ramus mentalis externus facialis
r.ment. V ramus mentalis V
r.m.i.f. ramus mentalis internus facialis
r.n.e. V ramus nasalis externus profundu
r.n.i. V ramus nasalis internus profundu
r.o.f. ramus oticus facialis
r.o.p. V ramus ophthalmicus profundus
r.pal.f. ramus palatinus facialis
r.p. IX ramus pharyngeus IX
r.rec.i. X ramus recurrens intestinalis X
r.rec.l. X ramus recurrens laryngeus X
r.s. ramus supratemporalis
r.s.o.f. ramus superior ophthalmicus faci
r.tr.i. ramus truncus infraorbitalis

s.a. stapedial artery
sc.c. sclerotic cartilage
s.l.o.v. superior lateral orbital vein
s.n. I–V spinal nerves I–V
s.o.a. supraorbital artery
s.o.f. supraorbital foramen
som. somite
sph.l. sphincter laryngeus
syn.j. syndesmotic joint

t.c. trabecula cranii
t.h. trabecular horn
thorhy. thoracicohyoideus muscle
t.i.a. X truncus-intestino-accessorius X
t.int. tectum internasale
t.m.p. taenia marginalis posterior
t.na. tectum nasale
t.p. trabecula plate
tr. trachea
trans. IV transversus ventralis IV
trap. trapezius
t.s. tectum synoticum

v.a. vertebral artery
v.c.l. vena capitis lateralis
v.c.m. vena capitis medialis
vert. I, II, III vertebra I, II, III
v.g. vagus ganglion

X
cialis

s V
ris anterior V
ris posterior V

V
from r. mandi-

s facialis

facialis
profundus V
orofundus V

ofundus V

inalis X
geus X

nicus facialis
lis

ein

e
orius X

or

V

I

e.c.a. external carotid artery

e.n. external naris

exocc. exoccipital bone

f.ab. foramen abducentis

f.ap. foramen apicale

f.ant. foramen anterior of nasal capsule

f.b. fore-brain

l.i.r. X lateralis inferior ramus X

l.m.a. levator mandibulae anterior

l.m.e. levator mandibulae externus

l.m.p. levator mandibulae posterior

l.o.n. lamina orbito-nasalis

lrx. larynx

l.s.r. X lateralis superior ramus X

l.v.r. X lateralis ventralis ramus X

p.t. pars trachealis

r. rib
r.a. ramus auricularis
r.a.f. ramus alveolaris facialis (r. mandibularis internus facialis)
r.b.f. ramus buccalis facialis
r.c. X ramus cardiac X

v.c.m. vena capitis medialis
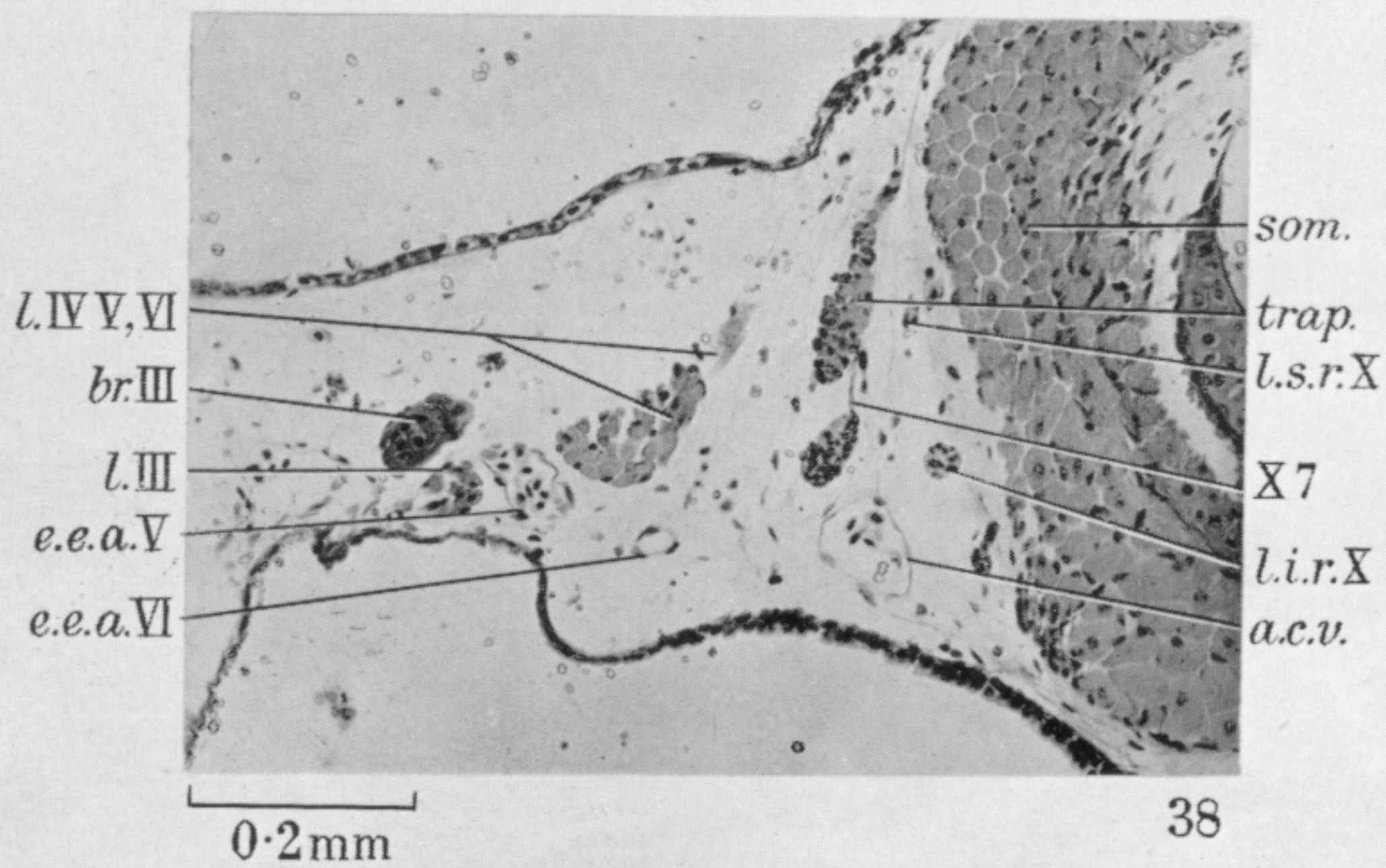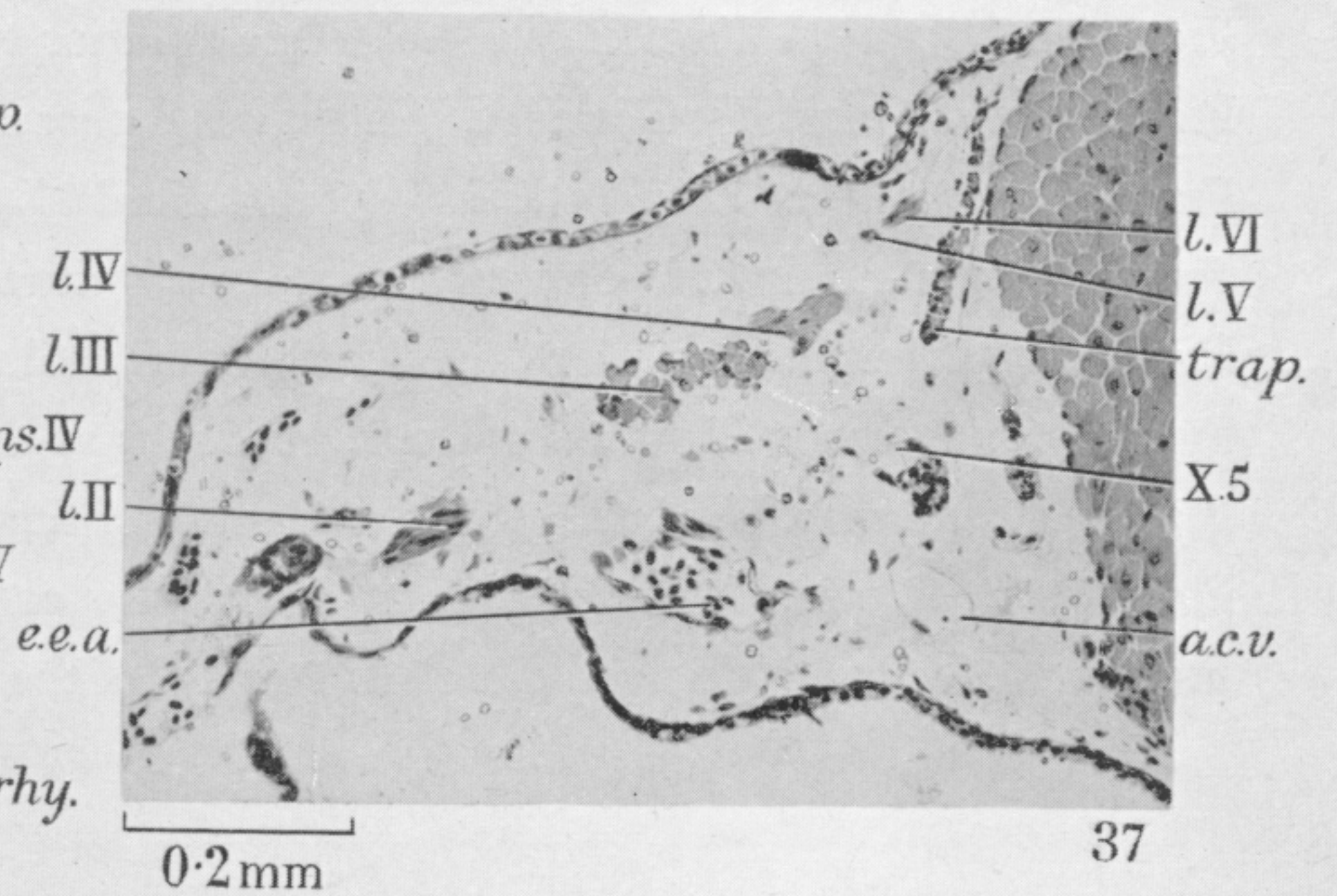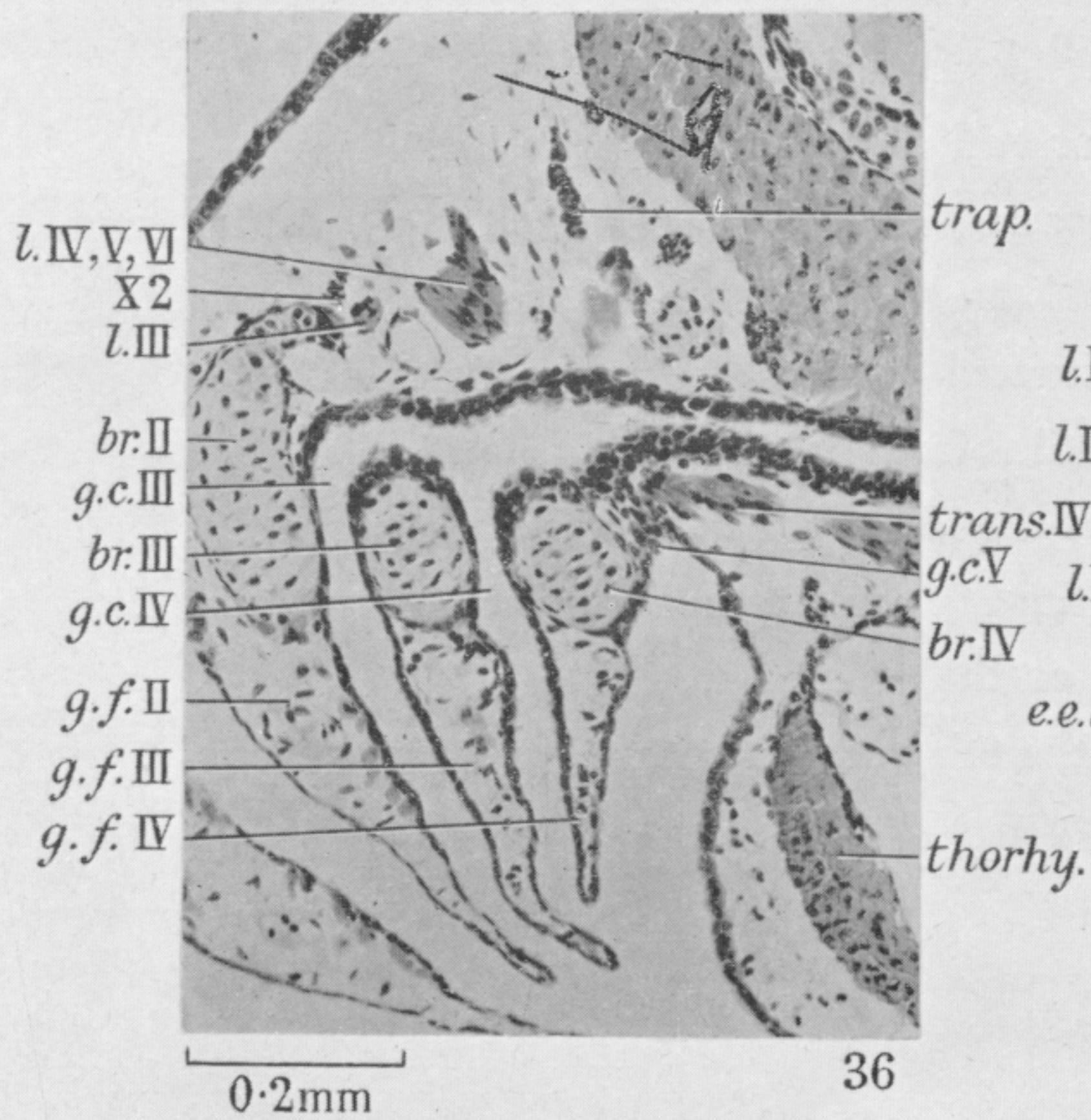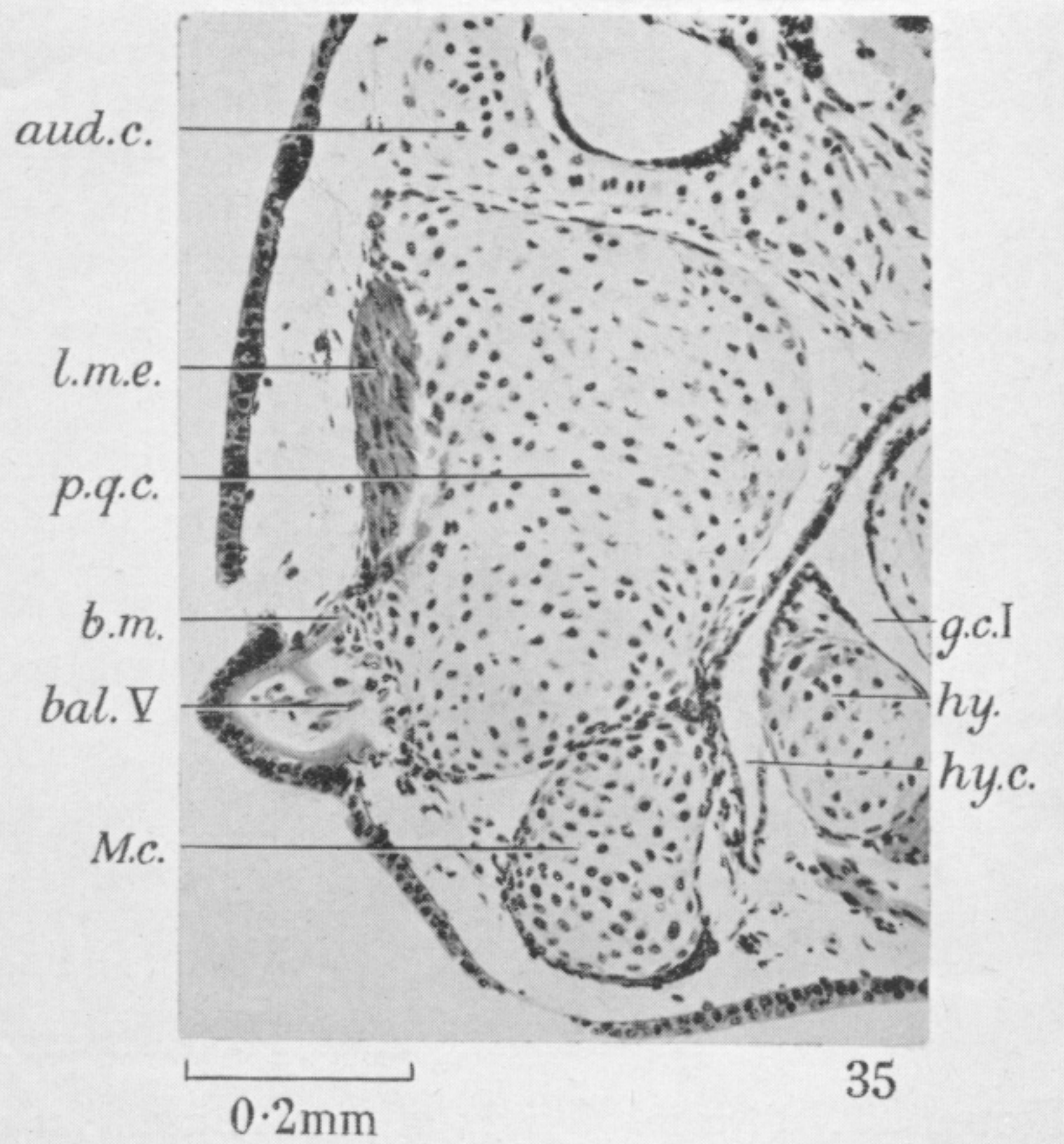*vert.* I, II, III vertebra I, II, III
v.g. vagus ganglion
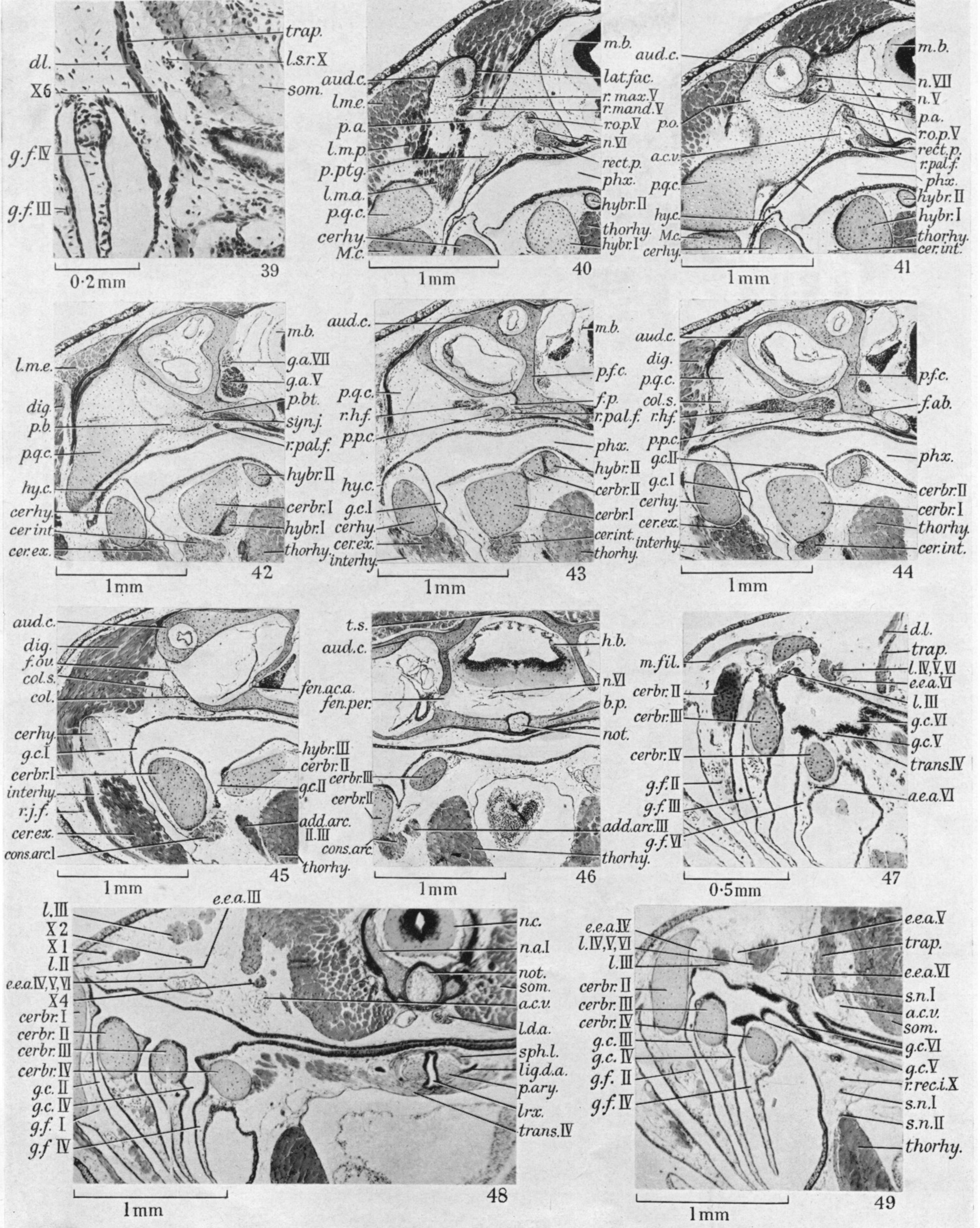*v.r.vert.* I, vestigial rib of vertebra I
v.v. vertebral vein

$\left.\begin{array}{l} x.\ 1\text{--}7 \\ X\ 1\text{--}7 \end{array}\right\}$ vagus nerves I–VII

I

ra I

Figures 34 to 38

Figure 39: scale 0·2 mm — labels: *dl.*, *X 6*, *g.f. IV*, *g.f. III*, *trap.*, *l.s.r. X*, *som.*

Figure 40: scale 1 mm — labels: *aud.c.*, *l.m.e.*, *p.a.*, *l.m.p.*, *p.ptg.*, *l.m.a.*, *p.q.c.*, *cerhy.*, *M.c.*, *m.b.*, *lat.fac.*, *r. max. V*, *r.mand. V*, *r.o.p. V*, *n. VI*, *rect.p.*, *phx.*, *hybr. II*, *thorhy.*, *hybr. I*

Figure 41: scale 1 mm — labels: *aud.c.*, *p.o.*, *a.c.v.*, *p.q.c.*, *hy.c.*, *M.c.*, *cerhy.*, *m.b.*, *n. VII*, *n. V*, *p.a.*, *r.o.p. V*, *rect.p.*, *r.pal.f.*, *phx.*, *hybr. II*, *hybr. I*, *thorhy.*, *cer.int.*

Figure 42: scale 1 mm — labels: *l.m.e.*, *dig.*, *p.b.*, *p.q.c.*, *hy.c.*, *cerhy.*, *cer.int.*, *cer.ex.*, *m.b.*, *g.a. VII*, *g.a. V*, *p.bt.*, *syn.j.*, *r.pal.f.*, *hybr. II*, *hy.c.*, *cerbr. I*, *hybr. I*, *thorhy.*

Figure 43: scale 1 mm — labels: *p.q.c.*, *r.h.f.*, *p.p.c.*, *hy.c.*, *g.c. I*, *cerhy.*, *cer.int.*, *thorhy.*, *aud.c.*, *m.b.*, *p.f.c.*, *f.p.*, *r.pal.f.*, *phx.*, *hybr. II*, *cerbr. II*, *cerbr. I*, *cer.ex.*, *interhy.*

Figure 44: scale 1 mm — labels: *g.c. II*, *g.c. I*, *cerhy.*, *cer.ex.*, *interhy.*, *aud.c.*, *dig.*, *p.q.c.*, *col.s.*, *r.h.f.*, *p.p.c.*, *p.f.c.*, *f.ab.*, *phx.*, *cerbr. II*, *cerbr. I*, *thorhy.*, *cer.int.*

Figure 45: scale 1 mm — labels: *aud.c.*, *dig.*, *f.ov.*, *col.s.*, *col.*, *cerhy.*, *g.c. I*, *cerbr. I*, *interhy.*, *r.j.f.*, *cer.ex.*, *cons.arc. I*, *fen.a.c.a.*, *fen.per.*, *hybr. III*, *cerbr. II*, *g.c. II*, *cerbr. I*, *add.arc. II. III*, *cons.arc.*, *thorhy.*

Figure 46: scale 1 mm — labels: *t.s.*, *aud.c.*, *cerbr. III*, *cerbr. II*, *h.b.*, *n. VI*, *b.p.*, *not.*, *add.arc. III*, *thorhy.*

Figure 47: scale 0·5 mm — labels: *m.fil.*, *cerbr. II*, *cerbr. III*, *cerbr. IV*, *g.f. II*, *g.f. III*, *g.f. VI*, *d.l.*, *trap.*, *l. IV, V, VI*, *e.e.a. VI*, *l. III*, *g.c. VI*, *g.c. V*, *trans. IV*, *a.e.a. VI*

Figure 48: scale 1 mm — labels: *l. III*, *X 2*, *X 1*, *l. II*, *e.e.a. IV, V, VI*, *X 4*, *cerbr. I*, *cerbr. II*, *cerbr. III*, *cerbr. IV*, *g.c. II*, *g.c. IV*, *g.f. I*, *g.f. IV*, *e.e.a. III*, *n.c.*, *n.a. I*, *not.*, *som.*, *a.c.v.*, *l.d.a.*, *sph.l.*, *lig.d.a.*, *p.ary.*, *lrx.*, *trans. IV*

Figure 49: scale 1 mm — labels: *e.e.a. IV*, *l. IV, V, VI*, *l. III*, *cerbr. II*, *cerbr. III*, *cerbr. IV*, *g.c. III*, *g.c. IV*, *g.f. II*, *g.f. IV*, *e.e.a. V*, *trap.*, *e.e.a. VI*, *s.n. I*, *a.c.v.*, *som.*, *g.c. VI*, *g.c. V*, *r.rec.i. X*, *s.n. I*, *s.n. II*, *thorhy.*
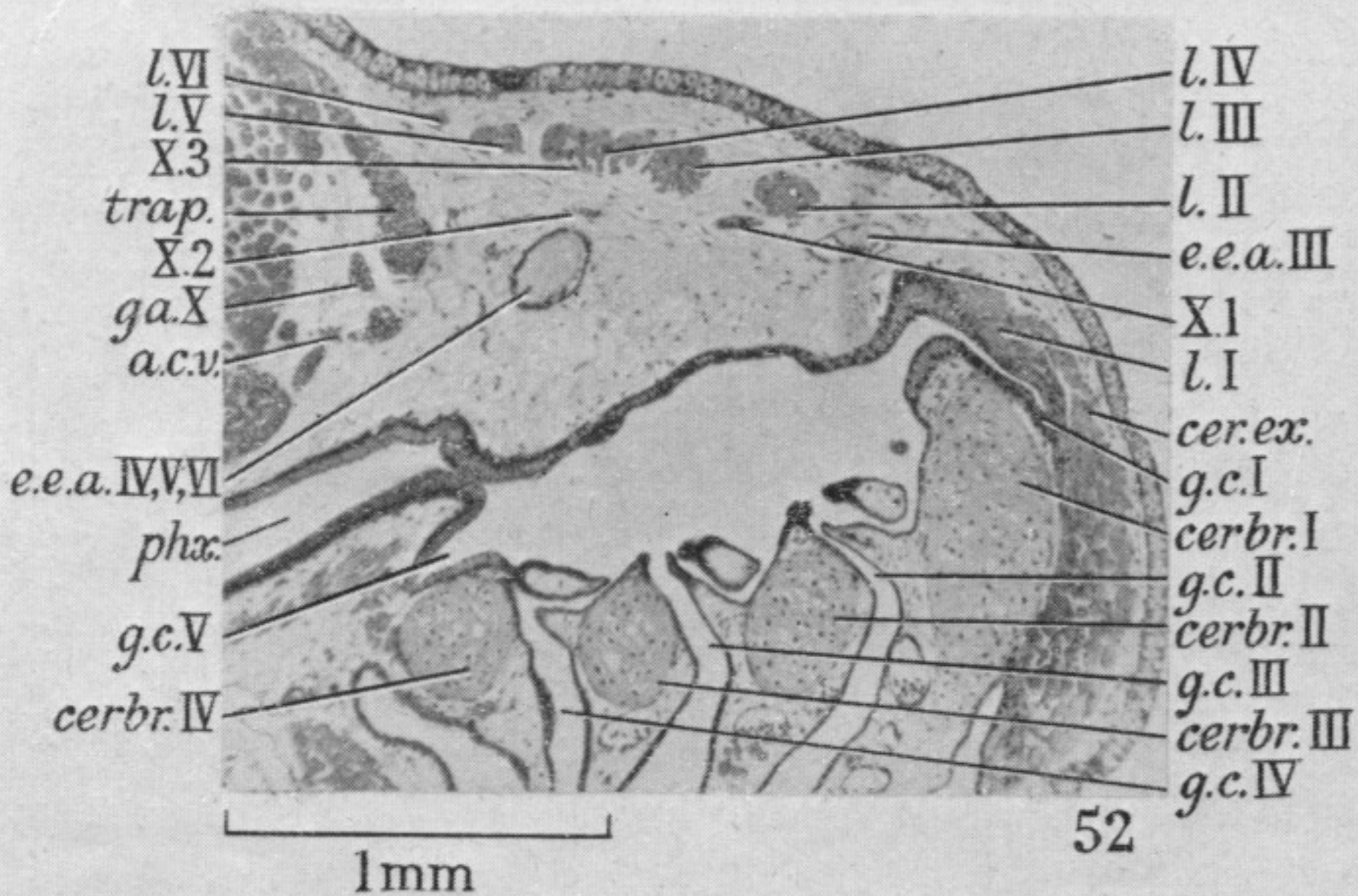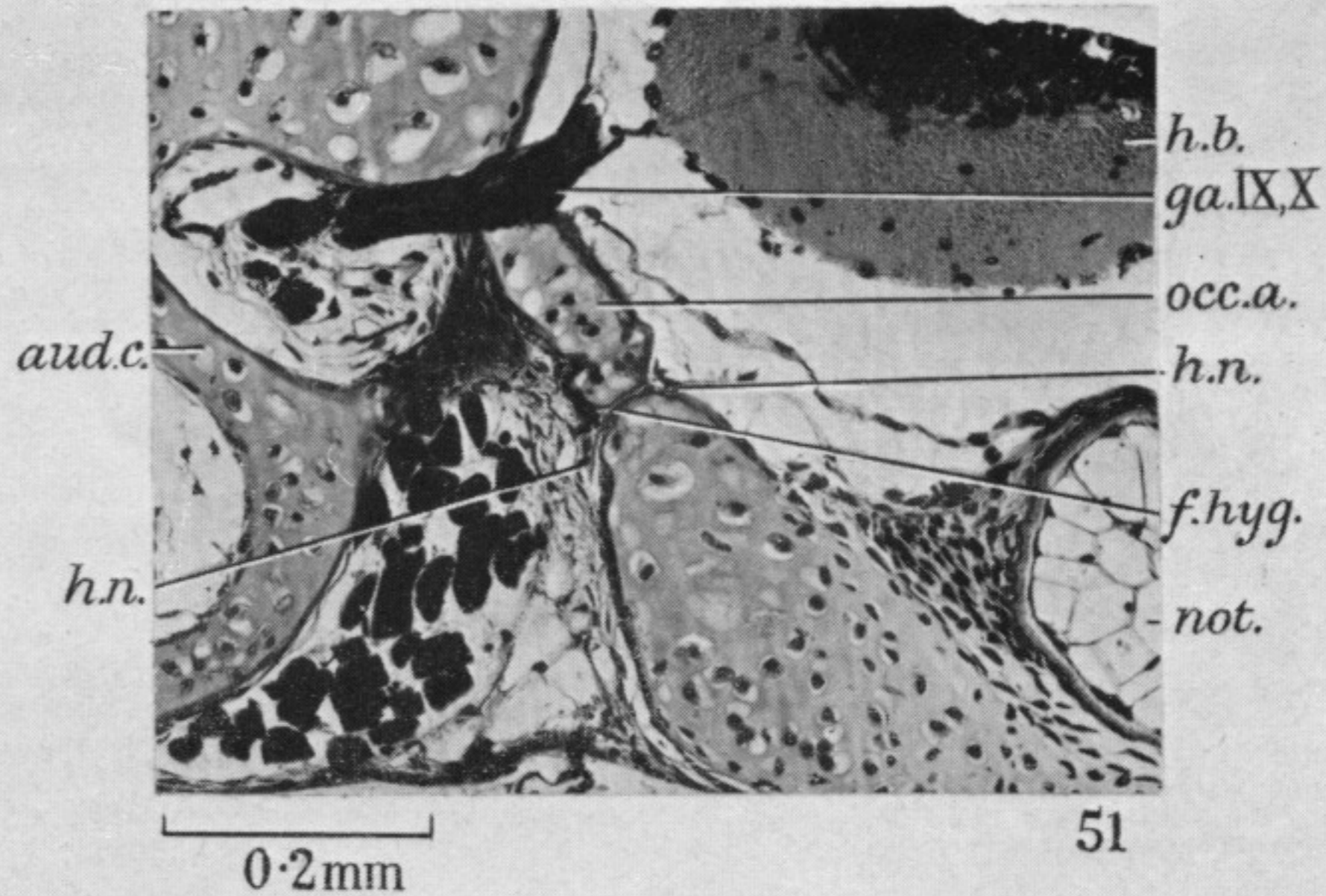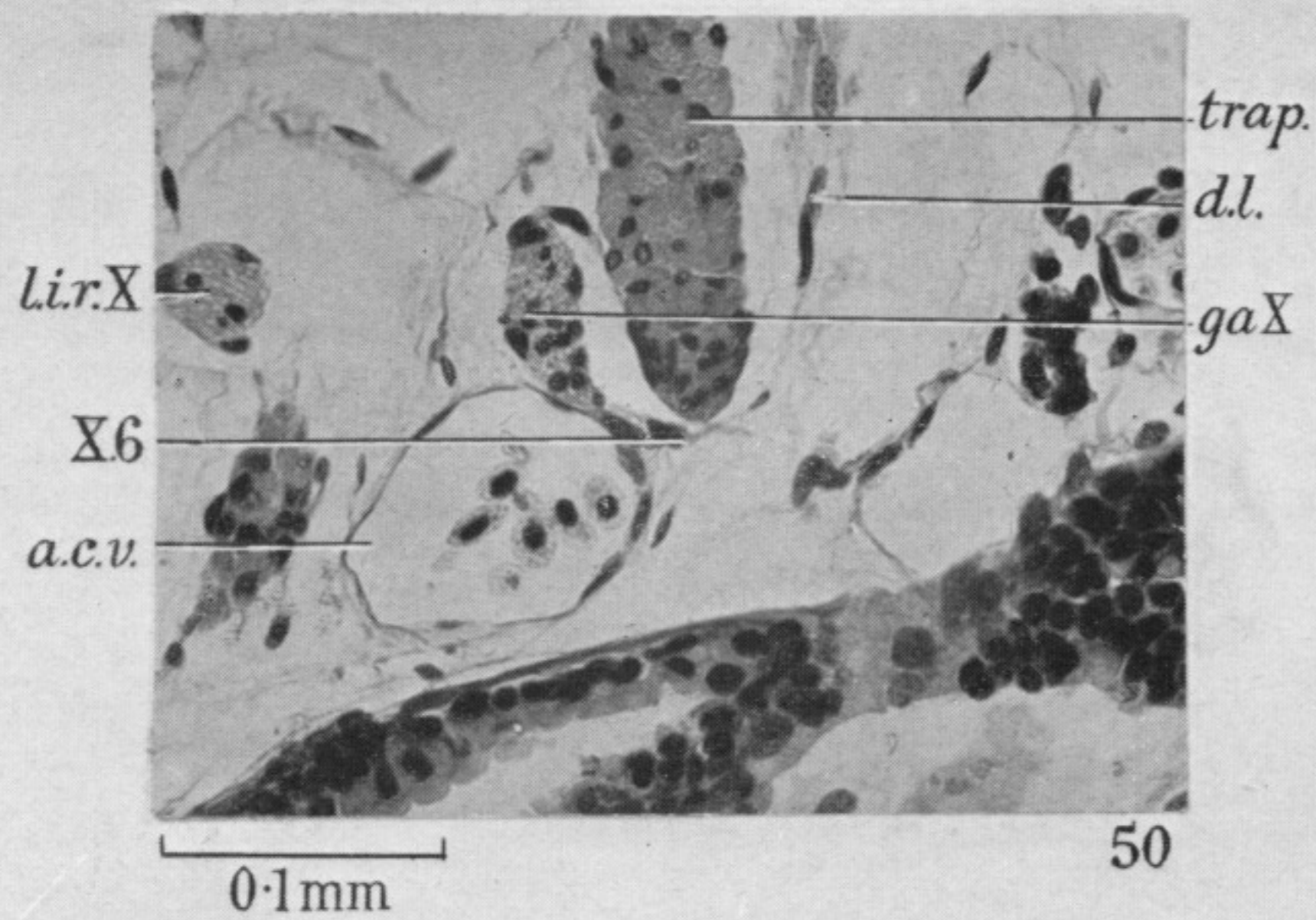
FIGURES 39 TO 49

FIGURES 50 TO 56

a.a.f. anterior auditory fenestra
a.c.c.a. anterior carotis cerebralis artery
a.cop. anterior copula
a.c.v. anterior cardinal vein
add.arc. II, III adductor arcuate muscles II, III
a.e.a. III–IV, V, VI afferent epibranchial arteries III–VI
aud.c. auditory capsule
aud.v. auditory vesicle

b.a. artery basalis
bal. V balancer nerve of r. mandibularis V
b.comm. basicapsular commissure
b.m. balancer membrane
br. I, II, III, IV branchiale I–IV
b.r.o.p. V branch of r. ophthalmicus profundus V
br.p. branchial plate
b.p. basal plate

cav.i. cavum internasale
cerbr. I, II, III, IV ceratobranchiale I–IV
cer.ex. ceratohyoideus externus
cerhy. ceratohyale
cer.int. ceratohyoideus internus
c.ob. cartilago obliqua
col. columella
col.s. columella stilus
com.t. commissura terminalis
cond. occipital condyle
conn. VII–IX Connective of Willis
con.arc. I, II, III, IV constrictor arcuate muscles I–IV
cop. copula
c.p.i.l. cartilago prenasalis inferior lateralis
c.ret. cartilago retronarina
c.s. crista sellaris
c.t. crista trabecula
c.v. cutaneous vein

d.a. dorsal aorta
d.C. ductus Cuvieri
dig. digastricus
dig.v. branch from VII–IX Conn. to digastricus
d.l. dilator laryngus
d.p. V deep profundus V

e. eye
e.e.a. III, IV, V, VI efferent epibranchial arteries III–VI
e.e.a.h. efferent epibranchial artery associated with the hyoid
e.c. ethmoidal column
e.c.a. external carotid artery
e.n. external naris
exoc. exoccipital bone

f.ab. foramen abducentis
f.ap. foramen apicale
f.ant. foramen anterior of nasal capsule
f.b. fore-brain

f.ch. fenestra choanalis
fen.ac.a. & p. fenestra acoustica anterior and posterior
fen.end.d. & v. fenestra endolymphatica dorsalis and ventralis
fen.per. fenestra perilymphatica
f.g. facialis ganglion
f.hy. foramen hyomandibularis
f.hyg. foramen hypoglossus
f.hyp. foramen hypophyseos
f.j. foramen jugulare
f.lat. fenestra lateralis nasi
f.na. fenestra narina
f.ol. foramen olfactorius
f.on. foramen orbito-nasalis
f.ov. fenestra ovalis
f.p. foramen palatinus
f.ps. foramen prootica

ga. V trigeminus ganglion
ge. VII facialis ganglion
ga. IX glossopharyngeal ganglion
ge. X vagus ganglion
ge.sn. II, III, IV ganglia spinal nerves II, III, IV
g.c. I–VII gill clefts I–VII
genhy. geniohyoideus muscle
g.f. I, II, III, IV external gill filaments I–IV
g.g. gasserian ganglion

h.b. hind-brain
h.n. hypoglossal nerve
ht. heart
hy. hyoid
hybr. I, II, III hypobranchiale I, II, III
hy.c. hyoid cleft
hyhg. hypohyale

i.c.a. internal carotid artery
i.l.o.v. inferior lateral orbital vein
inc.p. incisura prootica
interhy. interhyoideus muscle
int.m.ant. intermandibularis anterior

l. I–VI levator arcus branchialis I–VI
lat.conn. lateral cartilaginous connexion between neural arches
lat.fac. lateralis constituent of facialis ganglion
l.d.a. lateral dorsal aorta
l.f.g. lateralis facialis ganglion
lg. lung
lig.d.a. ligament of dilator laryngeus or arytenoid
l.i.r. X lateralis inferior ramus X
l.m.a. levator mandibulae anterior
l.m.e. levator mandibulae externus
l.m.p. levator mandibulae posterior
l.o.n. lamina orbito-nasalis
lx. larynx
l.s.r. X lateralis superior ramus X
l.v.r. X lateralis ventralis ramus X

m. mouth cavity
m.b. mid-brain
M.c. Meckel's cartilage
m.fil. external gill filament muscle
m.v. mandibular vein

n. III, IV, V, VII, IX oculomotor, trochlear, trigeminus, facialis and glossopharyngeal nerves
n.a. I, II, III neural arches I, II, III
n.c. nerve cord
n.cap. nasal capsule
n.oss. neural ossification
not. notochord
n.s. nasal sac
n.sp. II, III neural spines II, III
n.v. nasal vein

oc.a. occipital arch
oc.f. oculomotor foramen
oes. oesophagus
o.l. olfactory lobe
o.n. olfactory nerve
op.f. optic foramen
orb.v. orbital vein
o.v. optic vein

p.a. processus ascendens
pal.a. palatine artery
p.ary. arytenoid cartilage
p.b. processus basalis
p.bt. processus basitrabecularis
p.c.c.a. post-carotis cerebralis artery
p.cop. post-copula
p.cop.p. post-copula plate
p.c.s. post-cardinal sinus
p.c.v. post-cerebral vein
pec.pl. pectoral plexus
peric. pericardial cavity
p.fc. prefacial commissure
p.g. profundus ganglion
phx. pharynx
p.m.a.f. primary medial auditory foramen
p.o. processus oticus
post.z.n.a. II, III post-zygapophysis, neural arch II, III
p.p. pila prootica
p.p.c. post-palatine commissure
p.ptg. processus pterygoideus
p.q.c. pterygo-quadrate cartilage
p.r. prootic recess
prez.n.a. II, III prezygapophysis, neural arch II, III
p.t. pars trachealis

r. rib
r.a. ramus auricularis
r.a.f. ramus alveolaris facialis (r. mandibularis internus facialis)
r.b.f. ramus buccalis facialis
r.c. X ramus cardiac X

rect.p. rectus posterior
r.gast. X ramus gastricus X
r.g.t. X ramus gastrotrachealis X
r.h.f. ramus hyomandibularis facialis
r.hypob. ramus hypobranchialis
r.im. V ramus intermandibularis V
r.im.a. V ramus intermandibularis anterior V
r.im.p. V ramus intermandibularis posterior V
r.int. X ramus intestinalis X
r.j.f. ramus jugularis facialis
r.mand. V ramus mandibularis V
r.mass. V ramus to masseter from r. mandibularis V
r.max. V ramus maxillaris V
r.me.f. ramus mentalis externus facialis
r.ment. V ramus mentalis V
r.mi.f. ramus mentalis internus facialis
r.n.e. V ramus nasalis externus profundus V
r.n.i. V ramus nasalis internus profundus V
r.o.f. ramus oticus facialis
r.o.p. V ramus ophthalmicus profundus V
r.pal.f. ramus palatinus facialis
r.p. IX ramus pharyngeus IX
r.rec.i. X ramus recurrens intestinalis X
r.rec.l. X ramus recurrens laryngeus X
r.s. ramus supratemporalis
r.s.o.f. ramus superior ophthalmicus facialis
r.tr.i. ramus truncus infraorbitalis

s.a. stapedial artery
sc.c. sclerotic cartilage
s.l.o.v. superior lateral orbital vein
s.n. I–V spinal nerves I–V
s.o.a. supraorbital artery
s.o.f. supraorbital foramen
son. scnure
sph.l. sphincter laryngeus
syn.j. syndesmotic joint

t.c. trabecula cranii
t.h. trabecular horn
thorhy. thoracohyoideus muscle
t.i.a. X truncus-intestino-accessorius X
t.int. tectum internasale
t.m.p. taenia marginalis posterior
t.na. tectum nasale
t.p. trabecula plate
tr. trachea
trans. IV transversus ventralis IV
trap. trapezius
t.s. tectum synoticum

v.a. vertebral artery
v.c.l. vena capitis lateralis
v.c.m. vena capitis medialis
vert. I, II, III vertebra I, II, III
v.g. vagus ganglion
v.r.vert. I, vestigial rib of vertebra I
v.v. vertebral vein

v. 1–7 vagus nerves I–VII
X 1–7